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Article *in* Ecological Monographs · May 1996

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Ecological Monographs, 66(2), 1996, pp. 235–257
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HOST-PLANT SPECIALIZATION IN WESTERN PALEARCTIC ANTHIDIINE BEES (HYMENOPTERA: APOIDEA: MEGACHILIDAE)[1]

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Abstract. To determine the extent of host-plant specialization, the pollen sources of the 72 anthidiine species (family Megachilidae, subfamily Megachilinae, tribe Anthidiini) of Europe, North Africa, and Asia Minor were investigated by microscopic analysis of ≈1800 pollen loads of females. By this measure, 31 species (43%) were oligolectic (relatively specialized to pollen source) at the level of plant tribe, plant subfamily, or plant family. Exclusive pollen sources of these bees throughout their geographic ranges are flowers of the Cardueae (Compositae), the Asteroideae (Compositae), the Papilionoideae (Leguminosae), the Lamioideae (Labiatae), the Nepetoideae (Labiatae), the Dipsacaceae, or the Campanulaceae. Thirteen species (18%) were found to exhibit a strong, but not exclusive, preference for the Papilionoideae (Leguminosae), the Labiatae, the Cardueae (Compositae), and *Zygophyllum* (Zygophyllaceae), respectively, while 25 species (35%) proved to be more markedly polylectic, visiting the flowers of up to 17 different plant families for pollen. The plants exploited by three species (4%) are insufficiently known. By far the most important pollen sources of the anthidiine bees as a whole are the Compositae (41.7%) followed by the Leguminosae (23.1%) and the Labiatae (13.0%).

The phylogenetic relationships of the anthidiine bees were estimated by a cladistic analysis based on 115 characters to trace possible evolutionary patterns of diet composition. Based on the estimated phylogeny, at least eight shifts of oligoleges between different plant taxa and six transitions between oligolecty and polylecty appear to have occurred. Four transitions were from oligolecty to polylecty whereas two transitions are of unknown direction, both directions being equally parsimonious. Assuming that the ancestral state in the anthidiine bees was oligolectic, the present distribution of oligolectic and polylectic species can be explained solely by switches from the oligolectic to the polylectic habit and by shifts of oligoleges between different plant taxa. Three of four transitions from oligolecty to polylecty are accompanied by a reduction in bee body size. The significance of this size reduction with respect to the polylectic habit is discussed.

The oligolectic anthidiine species visit significantly fewer flower species for pollen during a single foraging bout than the polylectic species. On average, 1.4 plant species were recorded in the loads of specialists compared to 2.2 for generalists.

Two monophyletic groups of bees belonging to the genus *Anthidium* are equipped with a pollen-collecting apparatus consisting of specialized hairs localized either on the face or on the underside of the thorax. It is used to remove pollen from the raised anthers of flowers of the Labiatae and the Scrophulariaceae and to brush pollen from the flat inflorescences of some Compositae, respectively.

The observation of flower-visiting females of several anthidiine species revealed that pollen uptake is far from an accidental process. Basic pollen-harvesting techniques have reached a high degree of efficiency: females of a given bee species worked flowers of a certain plant species in a fixed manner, the structures used for pollen uptake from the same flower type were found to be largely the same among anthidiine bees of different taxonomic groups, and no distinct differences with respect to the basic pattern of pollen removal from flowers of the same architecture were obvious when comparing oligolectic and polylectic species. On the other hand, polyleges showed a high intraspecific flexibility regarding the organs used for pollen uptake from flowers of a different architecture.

Key words: anthidiine phylogeny; Apoidea; host-plant specializations; Megachilidae; oligolecty; pollen-foraging strategies; pollen-harvesting behavior; polylecty; western palearctic Anthidiini.

INTRODUCTION

Bees (Hymenoptera, Apoidea) feed their larvae with a mixture of pollen and nectar. Loew (1884) realized that certain bee species restrict foraging to flowers of a limited number of plants whereas others use a wide array of flowers. Robertson (1925) was the first to recognize that specialist bees demonstrate floral specificity only when harvesting pollen and not when licking nectar. He introduced the terms oligolectic and polylectic

[1] Manuscript received 3 April 1995; revised 22 June 1995; accepted 24 June 1995; final version received 28 July 1995.

TABLE 1. Anthidiine species investigated, their occurrence in the six geographic subareas, the desired number of pollen loads, and the actual number of loads examined. For each subarea in which the species occurs, the number of samples analyzed is given in brackets. The division of the study area into six subareas is shown in Fig. 1. For rare species or species living at the southern or eastern border of the study area, pollen loads from outside the study area were also examined. n = total number of pollen loads examined; N = number of loads from different localities.

Anthidiine species	Occurrence in the six geographic subareas						Loads from outside study area	Desired no. of pollen loads	No. of pollen loads examined	
	1	2	3	4	5	6			n	N
Trachusa pubescens (Morawitz, 1872)		[2]		[5]	[19]		[5]	25–35	31	23
Trachusa laeviventre (Dours, 1873)			[24]			[1]		20–30	25	19
Trachusa laticeps (Morawitz, 1873)			[1]	[13]	[2]			25–35	16	13
Trachusa byssina (Panzer, 1798)	[19]	[12]	[4]	[4]	[6]			35–45	45	40
Trachusa interrupta (Fabricius, 1781)	[8]	[0]	[7]	[11]	[19]	[0]		40–50	45	34
Trachusa dumerlei (Warncke, 1980)				[2]	[13]			20–30	15	11
Rhodanthidium aculeatum (Klug, 1832)					[23]		[1]	15–25	24	13
Rhodanthidium caturigense (Giraud, 1863)	[18]		[8]	[7]	[7]			30–40	40	33
Rhodanthidium exsectum (Pasteels, 1969)					[1]			15–25	1	1
Rhodanthidium superbum (Radoszkowski, 1876)					[24]		[11]	15–25	25	13
Rhodanthidium infuscatum (Erichson, 1835)			[22]	[1]		[8]		25–35	31	26
Rhodanthidium buteum (Warncke, 1980)					[1]			15–25	1	1
Rhodanthidium septemdentatum (Latreille, 1809)	[6]	[7]	[5]	[24]	[8]			35–45	50	49
Rhodanthidium acuminatum (Mocsary, 1884)				[2]	[2]			20–30	4	3
Rhodanthidium siculum (Spinola, 1838)			[5]	[4]		[21]		25–35	30	26
Rhodanthidium sticticum (Fabricius, 1787)			[10]	[6]		[19]		25–35	35	28
Anthidiellum strigatum (Panzer, 1805)	[7]	[11]	[12]	[18]	[4]	[5]		40–50	57	52
Anthidiellum breviusculum (Pérez, 1890)			[24]					15–25	24	16
Anthidiellum troodicum (Mavromoustakis, 1949)				[8]	[21]	[5]		25–35	34	27
Eoanthidium clypeare (Morawitz, 1874)				[14]	[8]			20–30	22	19
Eoanthidium judaeense (Mavromoustakis, 1945)					[5]		[1]	15–25	6	5
Eoanthidium nasicum (Friese, 1917)					[5]		[3]	15–25	8	8
Eoanthidium insulare (Morawitz, 1873)				[11]	[8]		[6]	20–30	25	18
Icteranthidium afrum (Lepeletier, 1841)						[9]		15–25	9	9
Icteranthidium laterale (Latreille, 1809)	[16]	[14]	[7]	[2]	[3]	[9]		40–50	51	43
Icteranthidium cimbiciforme (Smith, 1854)				[3]	[23]		[3]	20–30	29	21
Icteranthidium fedtschenkoi (Morawitz, 1875)					[0]		[20]	15–25	20	16
Icteranthidium grohmanni (Spinola, 1838)			[6]	[21]	[3]	[12]		30–40	42	36
Icteranthidium ferrugineum (Fabricius, 1787)			[6]		[6]	[21]	[2]	25–35	35	29
Icteranthidium limbiferum (Morawitz, 1875)					[5]		[15]	15–25	20	19
Icteranthidium ovasi (Warncke, 1980)					[4]		[3]	15–25	7	7
Afranthidium alternans (Klug, 1832)						[17]	[3]	15–25	20	13
Afranthidium schulthessi (Friese, 1897)			[13]			[10]		20–30	23	15
Afranthidium pusillum (Morawitz, 1895)					[11]		[2]	15–25	13	11
Afranthidium carduele (Morawitz, 1876)			[2]	[6]	[13]	[7]	[7]	30–40	35	25
Neanthidium octodentatum (Pérez, 1895)						[1]		15–25	1	1
Pseudoanthidium melanurum (Klug, 1832)			[11]	[9]	[2]	[4]	[4]	30–40	30	28
Pseudoanthidium rhombiferum (Friese, 1917)					[2]		[5]	15–25	7	6
Pseudoanthidium alpinum (Morawitz, 1874)		[1]		[1]	[0]			25–35	2	2
Pseudoanthidium lituratum (Panzer, 1801)	[6]	[9]	[4]	[14]	[7]	[15]		40–50	55	50
Pseudoanthidium ochrognathum (Alfken, 1932)						[13]	[7]	15–25	20	17
Pseudoanthidium reticulatum (Mocsary, 1884)			[7]	[16]	[4]	[2]	[1]	30–40	30	25
Pseudoanthidium eximium (Giraud, 1863)			[6]	[14]	[7]			25–35	27	17
Pseudoanthidium wahrmannicum (Mavromoustakis, 1933)						[12]	[8]	15–25	20	11
Anthidium pulchellum Klug, 1832						[1]	[4]	15–25	5	5
Anthidium echinatum Klug, 1832						[1]	[16]	15–25	17	13
Anthidium anguliventre Morawitz, 1888					[4]		[16]	15–25	20	15
Anthidium rotundum Warncke 1980					[2]		[3]	15–25	5	4
Anthidium undulatiforme Friese, 1917				[0]	[5]		[1]	20–30	6	5
Anthidium undulatum Dours, 1873				[17]	[8]		[2]	20–30	27	22
Anthidium oblongatum (Illiger, 1806)	[10]	[11]	[8]	[7]	[6]	[13]		40–50	55	55
Anthidium gussakovskiji Mavromoustakis, 1939					[7]		[1]	15–25	8	4
Anthidium tesselatum Klug, 1832						[2]	[17]	15–25	19	19
Anthidium waltlii Spinola, 1838						[4]	[13]	15–25	17	11
Anthidium wüstneii Mocsary, 1887					[9]		[4]	15–25	13	9
Anthidium caspicum Morawitz, 1880					[3]			15–25	3	1
Anthidium diadema Latreille, 1809			[6]	[10]	[14]	[9]		30–40	39	30
Anthidium spiniventre Friese, 1899				[13]	[7]		[3]	20–30	23	17
Anthidium luctuosum Gribodo, 1894						[9]		15–25	9	9
Anthidium trispinosum Friese, 1917					[4]			15–25	4	3
Anthidium punctatum Latreille, 1809	[10]	[14]	[8]	[4]	[7]	[4]		40–50	47	46

TABLE 1. Continued.

Anthidiine species	Occurrence in the six geographic subareas						Loads from outside study area	Desired no. of pollen loads	No. of pollen loads examined	
	1	2	3	4	5	6			*n*	*N*
Anthidium auritum Klug, 1832						[8]	[9]	15–25	17	12
Anthidium montanum Morawitz, 1864	[25]	[9]	[1]					25–35	35	32
Anthidium pullatum Morice, 1916						[5]		15–25	5	4
Anthidium cingulatum Latreille, 1809	[1]	[0]	[9]	[19]	[11]	[10]		40–50	50	49
Anthidium loti Ferris, 1852	[1]	[1]	[7]	[19]	[14]			35–45	42	35
Anthidium taeniatum Latreille, 1809			[9]	[11]	[10]	[10]		30–40	40	34
Anthidium dalmaticum Mocsary, 1884				[9]	[13]		[2]	20–30	24	19
Anthidium manicatum (Linnaeus, 1758)	[6]	[8]	[12]	[14]	[4]	[10]		40–50	54	52
Anthidium christianseni Mavromoustakis, 1956					[3]		[1]	15–25	4	4
Anthidium septemspinosum Lepeletier, 1841	[21]	[5]	[5]	[0]			[4]	30–40	35	25
Anthidium florentinum (Fabricius, 1775)	[0]	[2]	[18]	[18]	[7]			35–45	45	41

for relative pollen specialists and generalists, respectively. Females of oligolectic bees are characterized by consistently collecting pollen throughout the species' range and also in the presence of other pollen sources from only one plant species or from a group of related plant species, turning to other sources, if at all, only when there is a local shortage or absence of that pollen (Linsley and MacSwain 1958). Robertson's observation that oligolectic bees secure their nectar from many flowers while restricting themselves to a few species for pollen was confirmed by later authors (e.g., Linsley 1961, Stephen et al. 1969, Moldenke 1976, Michener 1979, Westrich 1989).

Oligolectic and polylectic species coexist in all investigated bee faunas. Their proportions, however, seem to vary markedly. The highest percentages of oligolectic bee species are observed in desert and mediterranean climates (>60% in California deserts, 40–50% in mediterranean California; Moldenke 1976, 1979*a, b*). Oligolecty appears to be less prevalent in more temperate regions (28% in southern Illinois, Robertson as cited in Michener 1979; 23% in Germany, Westrich 1989) and lowest in the tropics (17% in dry forest of Costa Rica, Heithaus 1979; 1–2% in moist tropical French Guiana, Michener 1979). Owing to the widespread coexistence of specialist and generalist bees, both oligolecty and polylecty obviously represent successful foraging strategies in evolutionary terms. Whereas polylecty is considered advantageous in reducing dependence upon a limited number of pollen sources (Michener 1954, Moldenke 1975, Eickwort and Ginsberg 1980), the factors that select for oligolecty or act to maintain it remain obscure. Several selective forces are discussed in the literature that are not mutually exclusive. Robertson (1899, 1925), Linsley (1958), and Michener (1954, 1979) assume that oligolecty has arisen to reduce interspecific competition for pollen. Their suggestion is based on the observation that the percentage of oligoleges is highest in the most species-rich bee assemblages. Lovell (1913, 1914) proposed instead that the higher foraging efficiency of specialist bees compared to generalists is the factor that selects for host specificity. Indeed, Strickler (1979), Cane and Payne (1988) and Laverty and Plowright (1988) showed that specialist bees handle their preferred flowers more efficiently than generalists. The differing biochemical composition of pollen and its relative nutritional value might be a further factor responsible for evolution and/or maintenance of the oligolectic habit. Several authors found the larvae of oligolectic or narrowly polylectic species to grow slowly or even to die on pollen not originating from their preferred host plants (Levin and Haydak 1957, Guirguis and Brindley 1974, Bohart and Youssef 1976). Similarly, Velthuis (1992) considers stabilization of larval food quality by concentrating on pollen of a few plant species the reason many bees became oligolectic.

The Anthidiini constitute a tribe of several hundred species in the subfamily Megachilinae of the Megachilidae (Roig-Alsina and Michener 1993). Apart from Antarctica and from Australia where only one species is known, anthidiine bees are distributed over all continents, each containing many genera and species (Michener and Griswold 1994). The nonparasitic members of this tribe are characterized by yellow, red, or white maculations on head, thorax, and abdomen ("metasoma"). Like all megachilids, the anthidiine females are provided with rows of stiff bristles on the underside of their metasoma forming a pollen brush or "scopa" in which the pollen is transported back to the nest. Depending on the species, the main cell-building material is either plant resin, which is sometimes combined with leaf stripes, plant fibers, soil particles and pebbles, or plant wool gathered from hairy leaves and stems (Michener 1948, Grigarick and Stange 1968, Pasteels 1977, Westrich 1989). The brood cells are built in excavated burrows in the soil or within preexisting cavities such as hollow stalks, rock fissures and empty snail shells, or they are freely attached to the surface of rocks, leaves, and stems.

With the exception of the few Central European species (Westrich 1989), the host-plant preferences of the

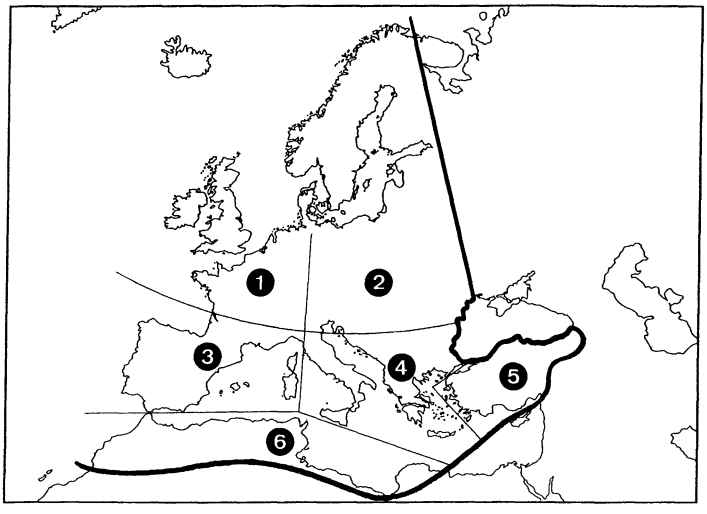

FIG. 1. Study area and its partition into six subareas. The Hoggar mountains in southern Algeria not shown on the map were part of the study area.

western palearctic anthidiine bees are virtually unknown. Based on microscopic analysis of scopal pollen contents of collected females, I examined the extent of oligolecty, the level of host-plant specialization, and the short-term specialization of individual females in the anthidiine bees of Europe, North Africa, and Asia Minor. A cladistic analysis of the bee species involved allowed me to trace the host-plant specializations in an evolutionary context (see Armbruster 1992) and to address the question of whether oligolecty or polylecty represents the derived foraging strategy in this bee group. I also investigated the existence of specialized morphological structures for pollen uptake and compared the pollen-harvesting behavior of oligolectic and polylectic species.

METHODS

Bee species

According to Warncke (1980), 71 species of the bee tribe Anthidiini (Apoidea: Megachilidae) occur in Europe, North Africa (inclusive Hoggar mountains), and Asia Minor (Fig. 1). I selected all 71 species for this study (Table 1).

Species delimitation and identification follows a monograph of the western palearctic anthidiine bees (Warncke 1980) with one exception. I consider *Anthidiellum breviusculum* Pérez to consist of two closely related, allopatric species: *A. breviusculum* Pérez in France, Portugal, and Spain, and *A. troodicum* Mavromoustakis in North Africa, Southeast Europe, and Asia Minor. The former species is characterized by hooked bristles on the labial palpi of the female lacking in the latter and by a mostly black female clypeus (lower part of the face) that is completely yellow colored in the other species. The nomenclature of the bee species follows Warncke (1980), and generic and subgeneric names conform to Michener and Griswold (1994).

I determined the approximate size of the female bees by measuring the length of the fore wing along its anterior margin in three randomly chosen specimens of each species.

Host-plant specializations

To assess the pollen plants of the 72 anthidiine species, I analyzed the scopal contents of ≈1800 females from museum, university, or private collections by light microscopy. The number of pollen loads examined per species depended on the range of each species within the geographic area considered in this study (Fig. 1). Species distributions were drawn from Warncke (1980) and from detailed unpublished maps of the same author.

I examined a basic number of 15 pollen loads per species independent of the size of its distribution area, plus additional five pollen loads for each of the geographic subareas in which the species occurs. Six geographic subareas of about equal size were delimited using biogeographic criteria (Fig. 1). I aimed to examine 40–50 pollen loads of species distributed in all six subareas and 15–25 loads of those occurring in only one subarea, respectively (see Table 1). For several rare species poorly represented in entomological collections, I could not examine the desired number of pollen loads. For each species, I attempted to include pollen samples from as many geographic localities as possible and to minimize the number of loads from specimens captured at the same locality and date.

I used the method of Westrich and Schmidt (1986) for pollen analysis. Before removing pollen from the female bees with a fine needle, I estimated the degree to which the metasomal scopae were filled. I assigned the pollen amounts to five classes ranging from 5 = full load to 1 = scopa one-fifth filled. After removing surface lipids by washing in ether, the pollen was embedded in glycerine gelatine on a slide. I estimated the percentages of different pollen types by counting the grains along four lines chosen randomly across the cover slip at a magnification of 400×. About 50–800 grains were counted per sample. Pollen types representing

TABLE 2. Host-plant spectrum of the 72 western palearctic anthidiine species. Percentages calculated from pollen grain counts of
CHE = Chenopodiaceae; CAR = Caryophyllaceae; POL = Polygonaceae; RAN = Ranunculaceae; PAP = Papaveraceae; CR
CRA = Crassulaceae; ROS = Rosaceae; LEG = Leguminosae (Pso = Psoraleeae, Hed = Hedysareae, Vic = Vicieae, Gen =
Loteae, Mim = Mimosoideae); ZYG = Zygophyllaceae; LIN = Linaceae; EUP = Euphorbiaceae; RUT = Rutaceae; CIS = Cis
= Myrtaceae; LYT = Lythraceae; UMB = Umbelliferae; PRI = Primulaceae; PLU = Plumbaginaceae; RUB = Rubiacea

Anthidiine species	CHE	CAR	POL	RAN	PAP	CRU	RES	CRA	ROS	LEG						
										Total	*Pso*	*Hed*	*Vic*	*Gen*	*Tri*	*Lot*
T. pubescens	..	..	..	..	..	..	..	..	..	0.3	..	..	..	..	..	..
T. laeviventre	..	..	..	..	..	..	..	..	1.2	80	3.8	..	..	4.8	..	..
T. laticeps	..	..	..	..	..	..	..	..	..	45.9	..	..	..	39.8	..	..
T. byssina	..	..	..	..	..	..	..	..	2.5	96.3	..	2.6	2.5	..	0.1	84.8
T. interrupta	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
T. dumerlei	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
R. aculeatum	..	..	..	..	..	..	..	..	..	0.3	..	..	..	..	..	0.3
R. caturigense	..	0.1	..	..	..	0.6	..	..	..	82.2	..	10.8	..	2.2	..	8.9
R. exsectum	..	..	..	..	..	..	..	..	..	96	..	..	..	..	..	..
R. superbum	..	..	..	..	..	..	..	..	..	97.7	..	13	0.1	..	..	..
R. infuscatum	..	..	..	..	..	5.8	..	10.9	..	20.6	0.3	1.3	..	1	0.4	4.8
R. buteum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
R. septemdentatum	..	..	..	0.4	0.6	0.3	..	7.1	1.3	33.4	0.3	4.2	4.4	3.1	0.4	10.5
R. acuminatum	..	..	..	..	..	..	..	..	..	73.6	..	39.6	..	..	..	..
R. siculum	..	..	..	0.5	11.3	1.4	..	..	..	14.5	..	..	2.4	..	..	5.2
R. sticticum	..	..	..	..	0.9	1.7	0.3	0.1	2.2	43.6	1	..	2.8	4.7	0.9	23.1
A. strigatum	..	..	..	..	..	0.5	1.1	0.8	2.6	70.2	..	2.9	..	3	0.8	42.1
A. breviusculum	..	..	..	..	..	..	..	0.8	..	1.1	..	..	..	..	..	..
A. troodicum	..	..	..	..	..	..	..	..	..	3.4	..	..	..	2.9	..	..
E. clypeare	..	..	..	..	..	6.9	..	..	..	22.5	..	4.3	..	8.6	..	1.9
E. judaeense	..	..	..	..	..	..	..	1.2	..	12.4	..	12.4	..	..	..	..
E. nasicum	..	..	..	..	..	1.3	20.1	..	..	5.4	..	0.7	..	..	..	..
E. insulare	..	..	..	..	7.2	0.4	..	..	1.8	20.3	2.8	4.5	..	6.2	..	..
I. afrum	..	..	..	..	..	..	..	..	..	6	..	..	..	..	..	..
I. laterale	..	..	..	..	..	1.1	..	0.4	2.3	2.2	..	..	..	..	..	0.4
I. cimbiciforme	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
I. fedtschenkoi	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
I. grohmanni	..	..	..	0.1	..	2.6	0.7	3.1	..	2.6	..	..	..	..	..	..
I. ferrugineum	..	0.4	..	..	..	10.1	0.5	3.6	..	18.6	..	2.5	..	..	..	12
I. limbiferum	12.3	3	..	..	..	11.4	..	..	..	24.6	8.7	..	..	..	0.9	..
I. ovasi	7.6	..	..	..	..	..	..	..	..	4.3	..	1.7	..	..	1.7	..
A. alternans	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
A. schulthessi	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
A. pusillum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
A. carduele	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
N. octodentatum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
P. melanurum	..	..	..	..	..	..	..	..	..	0.3	..	..	..	..	..	0.3
P. rhombiferum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
P. alpinum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
P. lituratum	..	..	..	..	..	0.1	..	..	..	..	..	..	..	..	..	..
P ochrognathum	..	..	0.7	..	..	51.6	..	..	..	17.9	..	..	..	..	..	3.6
P reticulatum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
P eximium	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
P. wahrmannicum	..	..	..	..	..	0.3	..	..	..	..	..	..	..	..	..	..
A. pulchellum	..	..	..	..	..	7.4	35.8	..	..	..	..	..	..	..	..	..
A. echinatum	..	..	..	..	..	17.5	..	..	..	..	..	..	..	..	..	..
A. anguliventre	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
A. rotundum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
A. undulatiforme	..	..	..	..	..	..	..	..	..	21.1	..	20	..	..	..	..
A. undulatum	..	..	..	..	..	..	..	..	0.1	80.7	1.4	3.4	..	..	..	29.5
A. oblongatum	..	..	..	..	..	..	20.6	11.7	0.8	48.5	..	9	..	..	..	30.5
A. gussakovskiji	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
A. tesselatum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
A. waltlii	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
A. wüstneii	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
A. caspicum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
A. diadema	..	..	..	..	..	..	..	..	..	3.3	..	..	..	0.2	2.2	..
A. spiniventre	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
A. luctuosum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
A. trispinosum	..	..	..	..	..	..	..	..	..	100	..	..	..	..	..	..
A. punctatum	..	..	..	..	..	0.2	7	2	..	85.5	..	13.1	..	1.6	4.2	56
A. auritum	..	..	..	..	..	14.3	20.6	..	..	21.2	..	..	..	..	11.2	8.9
A. montanum	..	..	..	..	..	..	..	..	..	99.6	..	..	0.2	..	0.1	84.7
A. pullatum	..	..	..	..	..	38.6	..	..	..	61.4	..	..	..	..	..	0.7
A. cingulatum	..	..	..	..	..	0.3	..	..	0.5	46.5	0.6	7.4	..	2.7	1.1	9.6
A. loti	..	..	..	..	..	..	..	..	..	76.3	..	6.5	..	..	..	21.7
A. taeniatum	..	..	..	..	..	0.1	..	..	..	72.2	..	0.1	..	3.9	..	47
A. dalmaticum	..	..	..	..	..	..	..	..	..	7.1	..	..	..	..	..	3.1
A. manicatum	..	..	..	..	..	..	..	..	..	43.6	..	0.3	..	2	1.6	4
A. christianseni	..	3.6	..	..	..	..	..	..	..	..	..	..	..	..	..	..
A. septemspinosum	..	..	..	..	..	..	..	2.5	17.7	26	..	..	4.3	..	9.9	1.7
						..	..	1	58.9	4.3	0.4	..	..	..	..	0.4

counts of female scopal contents are tabulated. Boraginaceae (Hel = Heliotropioideae, Bor = Boragineae, Lit = Lithospermeae); LAB = La
ceae; CRU = Cruciferae; RES = Resedaceae; (Rhi = Rhinanthoideae); ACA = Acanthaceae; PLA = Plantaginaceae; DIP = Dipsacacea
ae, Gen = Genisteae, Tri = Trifolieae, Lot = COM = Compositae (Car = Cardueae, Lac = Lactuceae, Ant = Anthemideae); LIL = Lilia
CIS = Cistaceae; CUC = Cucurbitaceae; MYR or tribe. (In the column headings, capital letters indicate plant families, small letters subfan
Rubiaceae; CON = Convolvulaceae; BOR = loads examined.

																		BOR				LAB		
i	*Lot*	Others	Mim	ZYG	LIN	EUP	RUT	CIS	CUC	MYR	LYT	UMB	PRI	PLU	RUB	CON	Total	Hel	*Bor*	*Lit*	Total	Lam	N
	..	0.3	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	99.3	99.2	(
	..	71.4	..	..	..	..	..	3.5	..	..	..	..	..	..	..	..	0.2	..	..	0.2	13.5	12.6	(
	..	6.1	..	..	..	..	..	1.2	..	2.7	..	..	..	..	..	..	..	..	..	..	44.8	22.2	2
.1	84.8	6.3	..	..	..	..	..	0.5	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
	..	..	..	..	..	..	..	0.1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
	0.3	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	99.7	..	9
	8.9	60.2	..	..	..	..	..	3.5	..	..	..	2.6	..	..	..	..	4.1	..	..	4.1	1.9	1.5	(
	..	96	..	..	..	..	..	..	..	..	..	4	..	..	..	..	..	..	..	..	..	..	
	..	84.6	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	2.3	1.5	(
.4	4.8	12.8	..	..	..	..	..	7.5	..	..	..	0.3	..	..	..	..	3.8	..	..	3.8	8	4.8	1
	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
.4	10.5	10.6	..	..	..	..	..	18	..	..	..	..	2.7	..	..	0.9	1.1	..	..	1.1	3.3	2.8	(
	..	34	..	..	0.9	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
	5.2	6.9	..	..	..	..	..	..	..	..	..	..	..	..	1.2	0.6	6.3	..	..	6.3	..	..	
.9	23.1	9.2	2	..	..	..	..	11.3	..	..	..	..	..	..	..	1	6.8	..	0.3	6.5	0.7	0.2	(
.8	42.1	21.4	..	..	..	..	..	0.3	..	..	0.2	0.5	0.1	..	0.2	..	0.3	..	..	0.3	6.7	6.3	(
	..	1.1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	91.7	48.9	4
	..	0.5	..	..	..	..	..	..	..	..	..	4.2	..	..	..	..	1.1	..	..	1.1	90.6	54.4	3
	1.9	7.8	..	..	..	..	..	..	..	..	..	5.6	..	..	..	..	5	..	..	5	8.8	3	
	..	..	..	..	..	..	..	..	..	..	..	0.6	..	..	..	..	..	..	..	..	..	..	
	..	4.7	..	..	..	..	..	..	..	..	..	5.4	..	..	..	..	1.3	..	..	1.3	41.6	32.2	
	..	6.9	..	..	..	..	..	0.9	..	..	..	..	..	..	..	..	9.5	..	..	9.5	10.1	3.7	(
	..	6	..	..	..	..	..	..	..	..	..	1.7	..	..	..	..	..	..	..	..	..	..	
	0.4	1.8	..	..	..	..	..	4.8	..	..	..	2.7	..	..	..	0.1	0.8	..	..	0.8	..	..	
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	..	2.6	..	..	..	..	..	0.3	..	..	..	35.7	..	..	..	..	1.6	1.1	0.3	0.2	9.1	3.3	
	12	4.1	..	0.3	..	..	1	..	2.7	..	..	8.6	..	1.9	..	..	4.5	1.6	..	2.9	8.3	8.3	
0.9	..	15	..	..	..	1.8	..	..	..	..	..	8.4	..	..	..	..	3.5	..	..	3.5	4.2	..	
1.7	..	1	..	..	..	..	..	..	..	..	3.1	3.1	..	..	..	..	1.2	1.2	..	..	..	..	
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..	0.3	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
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..	3.6	14.3	..	..	..	..	..	..	..	..	..	..	..	..	..	..	20.1	1.2	..	18.9	..	..	
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
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..	..	..	..	13.7	..	..	19.5	..	..	..	..	..	..	..	..	..	14.7	..	..	14.7	..	..	
..	..	..	..	82.5	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0.9	..	..	0.9	..	..	
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
..	..	1.1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1.4	..	..	1.4	77	77	
..	29.5	46.4	..	..	..	..	..	..	..	..	..	..	..	..	..	..	4.9	..	..	4.9	4.6	1.2	
..	30.5	9	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0.1	..	
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2.2	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1.7	..	..	1.7	..	..	
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..	..	100	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
4.2	56	10.6	..	..	..	..	..	1.4	..	..	..	..	..	..	..	..	..	..	..	..	0.4	0.2	
1.2	8.9	1.1	..	2.5	..	..	..	..	..	..	..	..	..	..	..	..	28.5	..	..	28.5	..	..	
0.1	84.7	14.6	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
..	0.7	60.7	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
1.1	9.6	25.1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	2.8	..	..	2.8	14.4	9	
..	21.7	48.2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	9.9	9.7	
..	47	21.3	..	..	..	..	..	..	..	..	..	1.4	..	..	..	..	1.3	..	..	1.3	9.1	8.3	
..	3.1	4	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	81.2	74	
1.6	4	35.7	..	..	..	..	..	..	..	..	0.2	..	..	..	..	..	1.2	..	..	1.2	36.2	27.5	
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	64	19.6	4
9.9	1.7	10.1	..	..	..	..	..	..	..	..	3.9	..	..	..	..	..	..	..	..	..	39.9	39.9	
..	0.4	3.4	..	..	..	..	..	..	..	..	5.6	2.9	..	..	..	..	4.6	..	1.8	2.8	16.5	11	

); LAB = Labiatae (Lam = Lamioideae, Nep = Nepetoideae); SCR = Scrophulariaceae
= Dipsacaceae (Dip = Dipsacoideae, Sca = Scabiosoideae); CAM = Campanulaceae;
; LIL = Liliaceae; ? = unknown; others = pollen types not attributed to any subfamily
etters subfamilies, and italics tribes.) Dots (··) indicate no pollen found in those pollen

	LAB		SCR					DIP				COM						
al	Lam	Nep	Total	Rhi	Others	ACA	PLA	Total	Dip	Sca	CAM	Total	*Car*	*Lac*	*Ant*	Others	LIL	?
.3	99.2	0.1	··	··	··	0.1	··	··	··	··	··	0.3	0.3	··	··	··	··	··
.5	12.6	0.8	1.6	··	1.6	··	··	··	··	··	··	··	··	··	··	··	··	0.1
.8	22.2	22.6	··	··	··	4.4	··	··	··	··	··	0.5	··	0.5	··	··	··	0.6
	··	··	··	··	··	··	··	··	··	··	··	0.1	··	0.1	··	··	··	0.6
	··	··	··	··	··	··	··	99.8	22.1	77.7	··	0.1	0.1	··	··	··	··	··
	··	··	··	··	··	··	··	··	··	··	··	100	100	··	··	··	··	··
.7	··	99.7	··	··	··	··	··	··	··	··	··	··	··	··	··	··	··	··
.9	1.5	0.4	1	··	1	··	··	··	··	··	··	1.4	1.4	··	··	··	··	2.6
	··	··	··	··	··	··	··	··	··	··	··	··	··	··	··	··	··	··
.3	1.5	0.8	··	··	··	··	··	··	··	··	··	··	··	··	··	··	··	··
	4.8	3.2	4.6	··	4.6	··	··	0.6	··	0.6	··	32.3	24.1	6.5	··	1.7	··	5.8
	··	··	··	··	··	··	··	··	··	··	··	100	88	12	··	··	··	··
.3	2.8	0.5	4.9	··	4.9	··	0.5	1.7	··	1.7	1.3	21.8	13.9	5.9	1.4	0.5	0.2	0.6
	··	··	··	··	··	··	··	··	··	··	··	25.5	25.5	··	··	··	··	··
	··	··	6.9	··	6.9	··	··	0.2	··	0.2	··	56.8	46.3	5.5	5	··	··	0.5
.7	0.2	0.5	6.7	··	6.7	··	··	··	··	··	··	21.8	7.7	13.3	0.8	··	2.1	0.7
.7	6.3	0.4	7.6	··	7.6	··	··	0.1	··	0.1	2.2	0.9	··	0.7	0.1	0.1	1.5	4.1
.7	48.9	42.8	2.4	··	2.4	··	··	··	··	··	3.9	··	··	··	··	··	··	··
.6	54.4	36.1	0.1	··	0.1	··	··	··	··	··	··	0.4	··	··	0.4	··	··	0.2
.8	3	5.8	11.3	··	11.3	··	··	··	··	··	0.4	1.1	··	0.3	0.2	0.7	38.3	0.1
	··	··	··	··	··	··	··	··	··	··	··	5.9	1.2	··	··	4.7	80	··
.6	32.2	9.4	··	··	··	··	··	··	··	··	··	9.1	4	··	5	··	14.8	1
.1	3.7	6.4	3.3	··	3.3	··	··	··	··	··	··	43.1	33.5	8.7	··	0.9	2.1	1.3
	··	··	··	··	··	··	··	··	··	··	··	92.3	92.3	··	··	··	··	··
	··	··	··	··	··	··	··	1.3	0.2	1.1	0.2	84.2	82.7	0.2	··	1.4	··	··
	··	··	0.8	··	0.8	··	··	··	··	··	··	99.2	98.9	0.3	··	··	··	··
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.1	3.3	5.7	6.7	··	6.7	··	··	2	··	2	0.7	31.5	26.2	2.1	2.1	1.1	0.6	2.8
.3	8.3	··	13.6	··	13.6	··	··	0.3	··	0.3	··	22.3	8.6	3.9	1	8.7	··	3.5
.2	··	4.2	··	··	··	··	0.3	··	··	··	··	26.1	7.5	5.1	0.6	12.9	0.2	4
	··	··	··	··	··	··	13.1	··	··	··	··	67.5	57.3	··	7.4	2.9	··	··
	··	··	··	··	··	··	··	··	··	··	··	100	··	··	49.9	50.1	··	··
	··	··	··	··	··	··	··	··	··	··	··	100	··	··	53.7	46.3	··	··
	··	··	··	··	··	··	··	··	··	··	··	100	··	··	92.8	7.2	··	··
	··	··	··	··	··	··	··	··	··	··	··	100	95.2	··	2.2	2.5	··	··
	··	··	··	··	··	··	··	··	··	··	··	96	86.7	··	··	9.3	··	4
	··	··	··	··	··	··	··	··	··	··	··	99.6	99.2	··	··	0.4	··	0.1
	··	··	··	··	··	··	··	··	··	··	··	100	100	··	··	··	··	··
	··	··	··	··	··	··	··	··	··	··	··	100	100	··	··	··	··	··
	··	··	··	··	··	··	··	··	··	··	··	99.9	84.1	3.2	3	9.6	··	··
	··	··	··	··	··	··	··	··	··	··	··	9.4	8	0.4	··	0.9	··	0.3
	··	··	··	··	··	··	··	··	··	··	··	99.9	99.9	··	··	··	··	0.1
	··	··	··	··	··	··	··	··	··	··	··	100	0.8	1.4	5.6	92.2	··	··
	··	··	··	··	··	··	··	··	··	··	··	99.7	··	··	··	99.7	··	··
	··	··	··	··	··	··	··	··	··	··	··	··	··	··	··	··	··	8.9
	··	··	··	··	··	··	··	··	··	··	··	··	··	··	··	··	··	··
	··	··	··	··	··	··	··	··	··	··	··	98.7	98.7	··	··	··	··	0.4
	··	··	··	··	··	··	··	··	··	··	··	100	100	··	··	··	··	··
7	77	··	··	··	··	··	··	··	··	··	··	··	··	··	··	··	··	0.5
4.6	1.2	3.3	6.3	··	6.3	··	··	··	··	··	··	0.2	0.2	··	··	··	··	3.2
0.1	··	0.1	1.1	··	1.1	··	··	··	··	··	14.9	··	··	··	··	··	2.2	··
	··	··	··	··	··	··	··	··	··	··	··	100	100	··	··	··	··	··
	··	··	··	··	··	··	··	··	··	··	··	100	··	··	··	100	··	··
	··	··	··	··	··	··	··	··	··	··	··	100	··	··	··	100	··	··
	··	··	··	··	··	··	··	··	··	··	··	100	··	··	··	100	··	··
	··	··	··	··	··	··	··	··	··	··	100	··	··	··	··	··	··	··
	··	··	··	··	··	··	··	··	··	··	··	95	94.9	0.1	··	··	··	··
	··	··	··	··	··	··	··	··	··	··	··	100	100	··	··	··	··	··
	··	··	··	··	··	··	··	··	··	··	··	100	100	··	··	··	··	··
	··	··	··	··	··	··	··	··	··	··	··	··	··	··	··	··	··	··
0.4	0.2	0.2	0.1	··	0.1	··	··	··	··	··	2.7	0.7	··	0.5	··	0.1	··	··
	··	··	3.2	··	3.2	··	··	··	··	··	··	5	··	1.6	3.4	··	··	4.6
	··	··	0.4	··	0.4	··	··	··	··	··	··	··	··	··	··	··	··	··
	··	··	··	··	··	··	··	··	··	··	··	··	··	··	··	··	··	··
4.4	9	5.4	18	1.8	16.2	··	··	··	··	··	0.4	15.9	10.4	4.6	··	0.8	··	1.2
9.9	9.7	0.2	12.1	0.1	12	··	··	··	··	··	··	··	··	··	··	··	··	1.7
9.1	8.3	0.8	14.2	··	14.2	··	··	··	··	··	··	0.1	··	··	0.1	··	··	1.5
1.2	74	7.2	9.4	··	9.4	··	··	··	··	··	··	··	··	··	··	··	··	2.3
6.2	27.5	8.7	16.7	··	16.7	··	··	··	··	··	··	2.1	2.1	··	··	··	··	··
4	19.6	44.4	8.4	··	8.4	··	··	··	··	··	10.4	13.6	7.6	6	··	··	··	··
9.9	39.9	··	7.9	2.2	5.7	··	··	··	··	··	··	1.2	0.4	··	··	0.8	··	0.7
6.5	11	5.5	1.1	··	1.1	··	··	··	··	··	··	3.7	3.7	··	··	··	0.1	1.3

<4% of counted grains were not considered in order to prevent biases caused by contamination. After assigning different weights to scopae according to how filled they were (full loads were five times more strongly weighted than scopas filled to only one-fifth), I summed the estimated percentages over all investigated samples of each species. I did not consider the volume of the pollen grains for correcting the percentages calculated from counts of the pollen types in mixed loads, because its calculation proved to be exceedingly time-consuming (see Tasei 1973, Buchmann and O'Rourke 1991, Silveira 1991).

In general, I determined the pollen grains to the family level at a magnification of 400× or 1000× with the aid of a reference collection consisting of pollen samples of ≈500 mainly mediterranean plant species and the identification aids in Zander (1935), Beug (1961), Maurizio and Louveaux (1965), Punt et al. (1976–1991), Sawyer (1981), Verlaque (1983), Faegri and Iversen (1989), and Moore et al. (1991). For five plant families rich in species and important as pollen sources for the bees investigated, the pollen grains were identified down to subfamily or tribe level whenever possible (see Table 2). Taxonomic subdivision of these families follows Polhill and Raven (1981) for the Leguminosae, Riedl (1967) for the Boraginaceae, Erdtman in Cantino (1992) for the Labiatae, Melchior (1964) for the Scrophulariaceae, and Caputo and Cozzolino (1994) for the Dipsacaceae. The names of the plant families conform to Brummitt (1992), and those of the plant species to Tutin et al. (1964–1980).

I judge the reliability of the pollen determinations as high. However, the small, tricolporate and reticulate pollen grains of many Scrophulariaceae were difficult to separate from those of *Hypericum* (Guttiferae), some Leguminosae, Solanaceae, and Zygophyllaceae. Grains of Resedaceae and Labiatae also can be very similar. Information about the plant species visited at the moment of capture written on the insect label was sometimes helpful. Otherwise, I assigned questionable grains to Scrophulariaceae rest and Resedaceae, respectively. Therefore, both families might be slightly over-represented. Pollen grains of *Vitex,* usually placed in the family Verbenaceae, were indistinguishable from the pollen of some Labiatae by the method outlined above. Thus, *Vitex* is included here in the subfamily Lamioideae of the Labiatae. Recently, Cantino (1992) considered *Vitex* to be a member of the Labiatae rather than of the Verbenaceae.

The assessment of host-plant preferences of a bee species by analyzing scopal contents is difficult without exact knowledge of all flowering plants available at the time of capture, unless the preferences are very strong. I define, therefore, only the following three classes of specialization: (1) *oligolectic*—95% or more of the counted pollen grains belong to one family, subfamily, or tribe; (2) *polylectic with a strong preference for one plant family*—70–95% of the counted grains belong to one family or tribe; (3) *polylectic*—no plant family is represented by >70% of the counted grains.

Phylogenetic relationships

For estimating the phylogenetic relationships of the anthidiine bees, I performed a cladistic analysis. A hypothesis on bee phylogeny allowed me to trace possible evolutionary patterns of diet composition.

The Anthidiini constitute a tribe in the subfamily Megachilinae of the Megachilidae (Roig-Alsina and Michener 1993). Their monophyly is well substantiated (Peters 1972, Michener and Griswold 1994). The tribes Megachilini and Osmiini, thought to have originated from a common ancestor, are believed to represent the sister group of the Anthidiini (Peters 1972, Michener and Griswold 1994). Peters (1972), in a discussion of the systematic position of *Aspidosmia* within the Megachilidae, concluded that this genus is the most primitive group of the Anthidiini and thus constitutes a candidate sister group of the remaining anthidiine species. Therefore, I selected two *Osmia,* one *Hoplitis* (both Osmiini) and two *Megachile* species (Megachilini), all of which have an Eurasian distribution, and a South African representative of *Aspidosmia* as outgroups for the cladistic analysis: *O.* (*Osmia*) *rufa* Linnaeus, *O.* (*Pyrosmia*) *submicans* Morawitz, *H. adunca* (Panzer), *M.* (*Delomegachile*) *willughbiella* (Kirby), *M.* (*Chalicodoma*) *pyrenaica* (Lepeletier), and *A. arnoldi* Brauns.

Adult bees of all species were examined externally with a dissecting microscope. I additionally dismembered the metasomae of the males to get appropriate views of the hidden sterna and the genitalia, and embedded the scopal hairs of the females in glycerine gelatine for microscopic study. Searching for morphological characters was facilitated by the publications of Michener (1948), Pasteels (1969), Warncke (1980), and Michener and Griswold (1994) where numerous characters are mentioned that proved to be appropriate for a phylogenetic study. In addition to the 111 morphological characters found, four biological characters drawn from Pasteels (1977) or originating from personal observations were also employed resulting in a total of 115 characters that went into the cladistic analysis (see Appendices 1 and 2).

The cladistic analysis was made on a Macintosh computer with PAUP (Phenetic analysis using parsimony) 3.1.1 (Swofford 1993) using the following heuristic search settings: simple and closest addition sequence, respectively, one tree held at each step during stepwise addition, TBR (tree bisection-reconnection) branch swapping, mulpars option in effect. All characters were treated as unordered and given the same weight with one exception. I gave character 99 (basal conjunction of the penis valves, see Appendix 1) double weight. The consequence of this differential weighting on the topology of the most parsimonious trees and its implication for tracing the probable evolution of the host-plant preferences are discussed in

Results: Phylogenetic relationships of the anthidiine bees.

After computing the most parsimonious trees with PAUP, I used the computer program MacClade 3.04 (Maddison and Maddison 1992) for exploring the evolution of host-plant preferences and reconstructing the evolution of some morphological traits thought to be connected with pollen uptake.

Short-term specialization of individual bees

I used the number of different pollen types per scopal content as a measure for the number of plant species visited for pollen during a single foraging bout. Pollen types representing <4% of counted grains were scored as contaminants. I judged the probability to be low that several plant species flowering at the same locality and date would have pollen grains indistinguishable from each other at a magnification of 400× or 1000×. It was assumed, therefore, that indistinguishable pollen grains within a sample belonged to one plant species. Only the absolute number of different pollen types in a given sample, but not their percentages, were considered.

The frequency distributions of the number of pollen types per load of oligolectic vs. polylectic species were tested for homogeneity applying chi square statistics. Classes were combined whenever necessary to satisfy the demand that the expected frequencies must be ≥1% in each class.

Specialized morphological structures

I carefully checked the females of all species under a dissecting microscope to detect specialized morphological structures that might be adaptations for extracting pollen from the flowers. Morphological structures presumed to play a part in pollen uptake were examined with a scanning electron microscope.

Pollen-harvesting behavior

I recorded pollen-harvesting behavior of females of 14 anthidiine species in the field using a threefold magnifying lens and a video camera. The field observations took place at different localities in Switzerland and Italy in the years 1992, 1993, and 1994. Voucher specimens of all species are deposited in my collection.

RESULTS

Host-plant specializations

Incidence of oligolecty and polylecty.—The results of analyzing ≈1800 pollen loads of the 72 anthidiine species are summarized in Table 2.

The species listed below can be classified as oligolectic (pollen plants in parentheses): *T. pubescens* (Lamioideae, Labiatae); *R. aculeatum* (Nepetoideae, Labiatae); *T. byssina, R. superbum,* and *A. montanum* (all Papilionoideae, Leguminosae); *T. interrupta* (Dipsacaceae); *I. cimbiciforme, I. fedtschenkoi, P. melanurum, P. reticulatum, A. anguliventre, A. diadema,* and *A. spiniventre* (all Cardueae, Compositae); *A. carduele* and *P. lituratum* (both Compositae with strong preference for Cardueae); *A. alternans, A. schulthessi, P. eximium, P. wahrmannicum, A. tesselatum,* and *A. waltlii* (all Asteroideae, Compositae). The following species are most probably oligolectic as well, although the number of analyzed pollen loads was smaller than desirable: *A. trispinosum* (Papilionoideae, Leguminosae); *T. dumerlei, P. rhombiferum, P. alpinum, A. rotundum, A. gussakovskiji,* and *A. luctuosum* (all Cardueae, Compositae); *A. pusillum* and *A. wüstneii* (both Asteroideae, Compositae); *A. caspicum* (Campanulaceae). In all, 31 anthidiine species (43%) appeared to be oligolectic.

T. laeviventre, R. caturigense, A. strigatum, A. undulatum, A. punctatum, A. loti, and *A. taeniatum* are all polylectic with a strong preference for Papilionoideae (Leguminosae). *A. breviusculum, A. troodicum,* and *A. dalmaticum* collect pollen predominantly but not exclusively on Labiatae. *I. laterale* and *A. echinatum* are both polylectic with a distinct preference for Cardueae (Compositae) and *Zygophyllum* (Zygophyllaceae), respectively. In spite of the small number of samples examined, *I. afrum* is considered to belong also to this group, as it is strongly dependent on Cardueae (Compositae); >90% of the counted pollen grains originated from this tribe. In all, 13 anthidiine species (18%) proved to be polylectic with a strong preference for one plant family.

No evidence of the spectrum of pollen plants can be given for *R. exsectum, R. buteum,* and *N. octodentatum* (4%), since only one pollen load per species could be analyzed.

The remaining 25 species (35%) were all found to be polylectic without strong preference for a single plant family. In *R. acuminatum, E. judaeense,* and *A. undulatiforme,* however, between 70% and 80% of the counted pollen grains belonged to one plant family. By reason of the small number of samples examined, these three species are assumed to be polylectic.

Species belonging to either polylectic class collect pollen on two (*A. echinatum*) to as many as 17 (*R. septemdentatum, A. strigatum*) different plant families (Table 2).

Level of host-plant specializations.—*T. byssina, R. superbum,* and *A. montanum* all collect pollen from several tribes of the subfamily Papilionoideae of the Leguminosae (Table 2). *T. interrupta* visits either subfamily of the Dipsacaceae. With the exception of *P. alpinum,* pollen grains of both the *Centaurea* and the *Cirsium/Serratula* type (Moore et al. 1991) representing different subtribes within the tribe Cardueae of the Compositae (Bremer 1994) were recorded in the pollen loads of all oligolectic species restricted to or exhibiting a distinct preference for the Cardueae. Plants of several tribes of the subfamily Asteroideae of the Compositae rank among the pollen sources of *A. alternans, A. schulthessi, A. pusillum,* and *P. eximium.* In *T. pu-*

bescens and *R. aculeatum,* pollen grains of the Lamioideae (Labiatae) and the Nepetoideae (Labiatae), respectively, found in the analyzed loads were of considerably different sizes and exine ornamentations. It seems highly probable that they stem from several genera in either case. Similarly, distinct differences in grain size and echinae shape and length in the pollen grains of the *Aster* type exclusively discovered in the pollen loads of *P. wahrmannicum, A. tesselatum, A. waltlii,* and *A. wüstneii* render it highly unlikely that these bee species are restricted to one plant genus or even species for pollen uptake. Only pollen grains of the Papilionoideae rest (Leguminosae) and of the *Centaurea* type (Cardueae, Compositae) were found in the four analyzed pollen loads of *A. trispinosum* and the two examined samples of *P. alpinum,* respectively. This small number of samples does not allow any conclusion regarding the level of host-plant specializations in these bees. The Campanulaceae on which *A. caspicum* is most probably specialized is a family poor in genera in the study area (Tutin et al. 1964–1980). Because pollen grains are very similar across this entire family, I was unable to attribute them to specific genera by the method of microscopic analysis used in this study. *A. caspicum,* therefore, might eventually prove to be specialized on genus level in future.

In summary, host-plant specializations in the anthidiine bees are exhibited at tribe, subfamily, or family level. Specializations on a lower level were not found with certainty in this bee group.

Host-plant spectrum of the Anthidiini.—The species investigated harvest pollen from the flowers of 32 different plant families (Table 2). Only a very few families, however, are represented in high percentages in the pollen plant spectrum of the Anthidiini as a whole. When summing the percentages of plant families found in the host-plant spectrum of each species (Table 2) over all species, the family Compositae contributes 41.7% and its tribe Cardueae 28.0% to the pollen-plant spectrum of the whole bee tribe. The Compositae are followed by the Leguminosae with 23.1% and the Labiatae with 13.0%. The pollen of Cruciferae, Scrophulariaceae, Liliaceae, Campanulaceae, Boraginaceae, and Resedaceae is represented by 2.8%, 2.5%, 2.1%, 2.0%, 1.9%, and 1.5%, respectively. These nine families include >90% of the plants the western palearctic anthidiine species visit for pollen. *R. exsectum, R. buteum,* and *N. octodentatum* were excluded from the calculation above since only a single pollen load per species could be analyzed.

Host-plant specializations in the context of anthidiine phylogeny

Phylogenetic relationships of the anthidiine bees.—The cladistic analysis resulted in 72 most parsimonious cladograms with a length of 249 steps, a consistency index of 0.55, and a retention index of 0.87. Analyses using both simple and closest addition sequence as search settings gave the same results. Strict and semistrict consensus trees are shown in Fig. 2. As a hypothesis on the phylogenetic relationships of the anthidiine species, the semistrict consensus tree is selected here for the purpose of tracing host-plant preferences in an evolutionary context and reconstructing the probable evolution of some morphological traits. In contrast to a strict consensus tree, which is derived by including only those components from a set of equally parsimonious trees that appear in all of the original trees, a semistrict consensus tree combines those components that are not contradicted (Bremer 1990). Semistrict consensus trees may thus contain greater resolution than strict consensus trees but do not smooth conflicting tree topologies as do Nelson or Adams consensus trees.

Character 99 (basal conjunction of the penis valves, see Appendix 1) was given weight 2 in the analysis. Both Pasteels (1969) and Michener and Griswold (1994) stress the systematic importance of this character. Its stronger weighting results in the monophyly of the genus *Anthidium,* which is widely accepted by several authors (Pasteels 1969, Michener and Griswold 1994). All other characters went into the analysis with weight 1 (see *Methods*). With equal weighting of character 99, the data matrix yielded 192 most parsimonious cladograms with a length of 248 steps, a consistency index of 0.55, and a retention index of 0.87. The semistrict consensus tree of the 192 equally parsimonious cladograms shows no conflicting topology when compared with that of the first analysis. Its resolution is lower, however, in that six monophyletic groups form a polytomy in contrast to the tritomy observed in the semistrict consensus tree derived from the first analysis. The results, which are derived from the semistrict consensus tree of the first analysis, were not found to contradict those obtained by use of the second semistrict consensus tree.

Host-plant specializations with respect to anthidiine phylogeny.—The three classes of host-plant specialization ("*oligolectic*", "*polylectic with strong preference for one plant family*" and "*polylectic*") are mapped onto the semistrict consensus tree in Fig. 3 using the assumption of parsimony, viz. minimal evolutionary change. The ingroup node was forced to be equivocal regarding the three classes of specialization by artificially assigning one of the three different states to each species of the outgroup.

T. pubescens, T. laeviventre, and *T. laticeps* constitute a monophyletic group of three closely related species (subgenus *Archianthidium*). The first restricts pollen foraging to the Labiatae whereas the other two also harvest pollen on other plant taxa, especially Leguminosae (Table 2). *T. laeviventre* even shows a strong preference for the latter family. On grounds of the estimated phylogenetic relationships, no decision is possible on the degree of host-plant specialization in the ancestor of this clade. A change from oligolecty to

polylecty is thus equally parsimonious as a transition from polylecty to oligolecty.

T. byssina, T. dumerlei, and *T. interrupta* are all oligolectic. The two latter species are nearest relatives belonging to the subgenus *Paraanthidium.* One of them is specialized on Cardueae (Compositae), the other collects pollen exclusively on Dipsacaceae demonstrating a clear transition of oligoleges between different plant taxa. The more distantly related *T. byssina* (subgenus *Trachusa*) gathers pollen only on Leguminosae making a further shift between different plant taxa most probable.

R. aculeatum is the sister species of the other *Rhodanthidium,* the *Anthidiellum,* and the *Eoanthidium* species. It is an oligolege of Labiatae. *R. superbum* (subgenus *Meganthidium*) collects pollen exclusively and *R. caturigense* (subgenus *Asianthidium*) predominantly on Leguminosae. The sole pollen load analyzed of *R. exsectum* (subgenus *Asianthidium*), a close relative of *R. caturigense,* consisted 96% of pollen of the Leguminosae, demonstrating a probable predilection for this plant family as well. The remaining *Rhodanthidium* species constitute a tight monophyletic group (subgenus *Rhodanthidium*). Apart from *R. buteum,* whose host-plant spectrum is unknown because only one pollen sample was available for study, they are all polylectic visiting up to 17 different plant families. By reason of the high percentages of Leguminosae pollen recorded for *R. caturigense, R. exsectum,* and *R. superbum,* which is in sharp contrast to the highly diverse pollen plant spectra observed in the five bees of *Rhodanthidium* s. str., the ancestral state in this clade is assumed to be oligolectic. Coding *R. caturigense* as oligolectic due to its highly developed predilection for Leguminosae leads to a clear support for an evolutionary transition from oligolecty to polylecty.

All three *Anthidiellum* species are characterized by a distinct preference for the pollen of a single plant family. The two allopatric species *A. breviusculum* and *A. troodicum* heavily depend on Labiatae whereas their close relative *A. strigatum,* which is sympatric with both the others, visits mainly Leguminosae in addition to many other taxa. The latter taxa, however, constitute only a small fraction of the host-plant spectrum of this species.

The four species belonging to the genus *Eoanthidium* are polylectic visiting up to ten plant families. Pollen of the family Liliaceae was represented with rather high percentages in the pollen loads of all these species indicating either a genetically based predilection and/or the occurrence in habitats rich in Liliaceae. *E. clypeare* was actually observed on hot and dry slopes in mediterranean Italy in summer where *Allium sphaerocephalon* grew in dense stands.

Regarding the range of plants visited for pollen, the morphologically uniform species of *Icteranthidium* can be divided into two groups. One group collects pollen exclusively (*I. cimbiciforme, I. fedtschenkoi*) or predominantly (*I. laterale, I. afrum*) on Cardueae (Compositae), and the other group consists of four polylectic species that harvest pollen from up to 15 plant families. Compared with other polylectic anthidiine species, pollen of Umbelliferae plays a rather important role in the larval nourishment of most of these bees, especially in *I. grohmanni.* A high percentage of the Umbelliferae pollen in the pollen loads examined turned out to stem from *Eryngium.* No clear decision is possible on the degree of host-plant specialization in the ancestor of *Icteranthidium* on grounds of parsimony. Nevertheless, the ancestral state is assumed to be oligolectic inferring a transition from oligolecty to polylecty within this group for the following reason. A slight relaxation of the oligolectic habit in *I. laterale* and *I. afrum* is more probable than the development of a strong but not entirely exclusive host-plant preference from a polylectic ancestor. Coding *I. laterale* and *I. afrum* as oligolectic due to their high preference for Cardueae (Compositae) reveals a change from oligolecty to polylecty within *Icteranthidium.*

All investigated species of *Afranthidium* and *Pseudoanthidium* are specialized on Compositae with one exception. *P. ochrognathum* is polylectic found to collect pollen on five different plant families, the most important being the Cruciferae, the Lithospermeae (Boraginaceae) and the Leguminosae. The pollen plant spectrum of *N. octodentatum* is insufficiently known since only a single pollen load was available. The pollen of Compositae was represented with 96% suggesting again a strong preference for this family. There is a clear difference between the oligolectic species with respect to the composites they visit for pollen. *A. carduele, P. reticulatum, P. melanurum, P. rhombiferum, P. alpinum,* and *P. lituratum* largely restrict pollen harvesting to the tribe Cardueae while *A. alternans, A. schulthessi, A. pusillum, P. eximium,* and *P. wahrmannicum* only exploit flowers of the subfamily Asteroideae (Fig. 4). The representatives of the Asteroideae possess disk-shaped inflorescences which are composed of numerous flowers densely packed in a single plane whereas the flower heads of the Cardueae are more loosely spaced. This difference in architecture may require different behavioral mechanisms for exploitation and may thus be responsible for the specialization of the bees on different composite taxa. An unequivocal change from oligolecty to polylecty can be observed within *Pseudoanthidium* with *P. ochrognathum* being the only polylectic species in this group. At least three transitions from Cardueae to Asteroideae or vice versa are supposed to have occurred within the genera *Afranthidium* and *Pseudoanthidium,* respectively (Fig. 4). The direction of these changes can in no case be determined using parsimony as a criterion, the ancestral states being equivocal.

A. pulchellum and *A. echinatum* are both polylectic, the latter showing a distinct preference for *Zygophyllum* (Zygophyllaceae). Besides *Zygophyllum,* only pol-

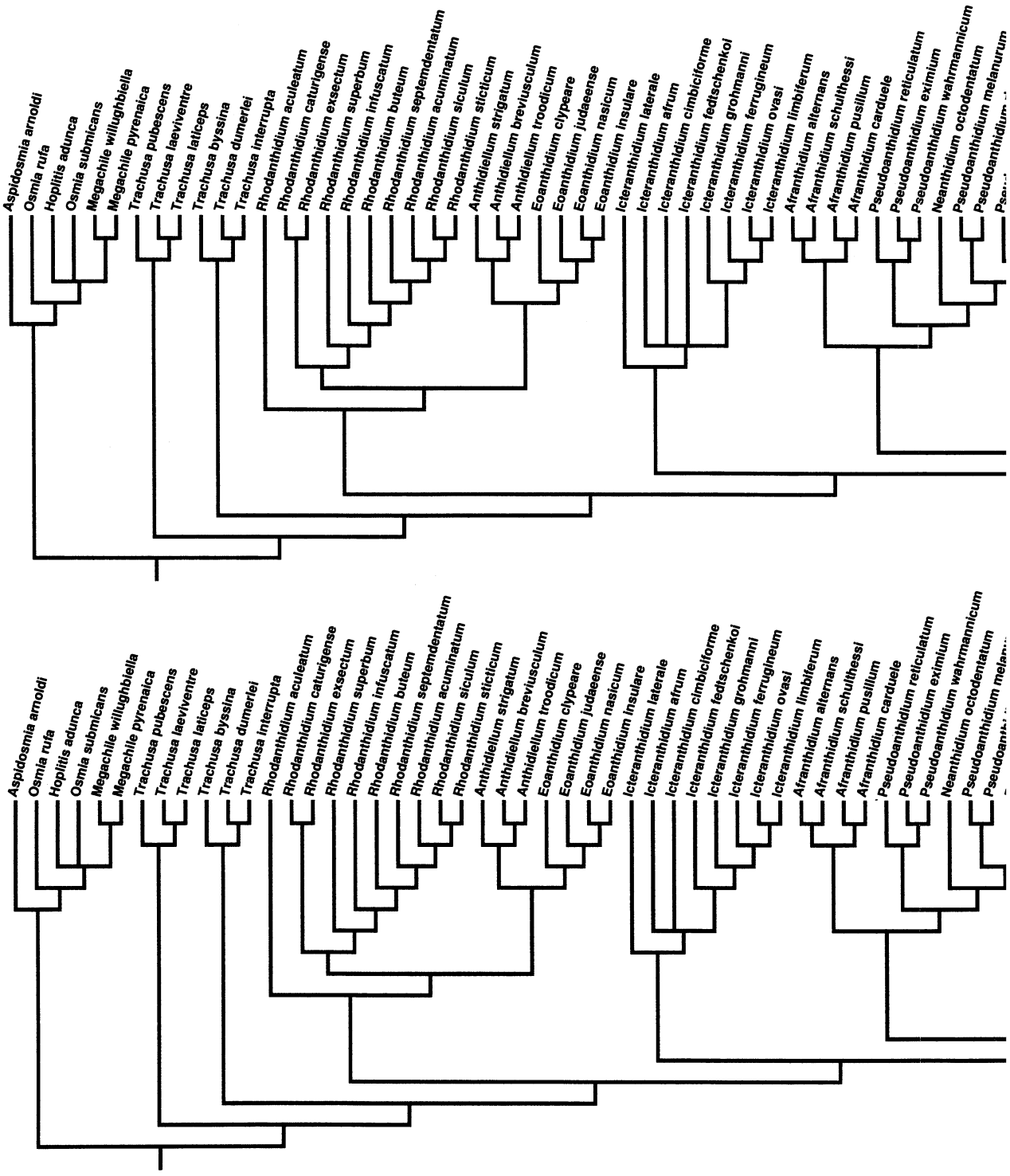
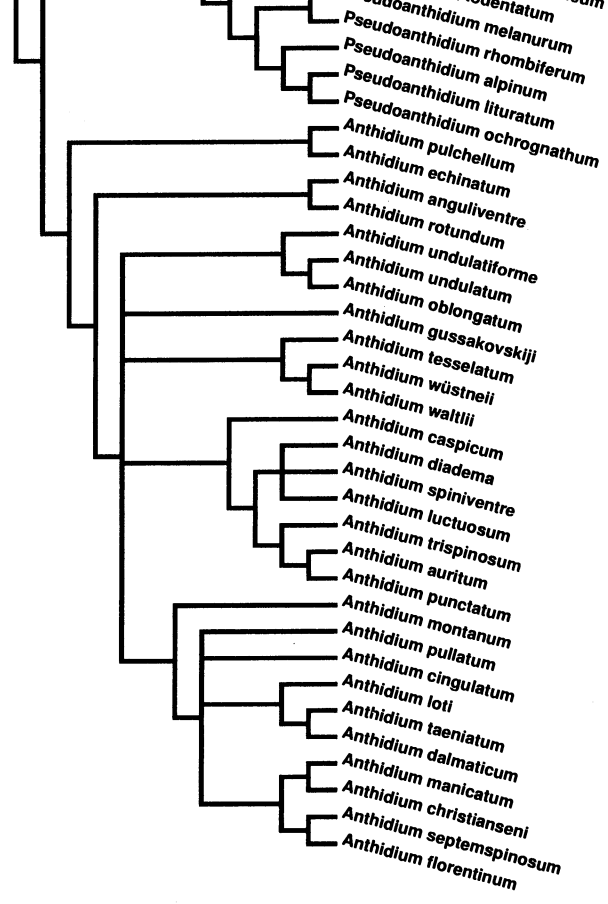


FIG. 2. Strict (above) and semistrict (below) consensus trees of 72 most parsimonious cladograms of the anthidiine bees. Character 99 (see Appendix 1) given double weight.

Pseudoanthidium octodentatum
Pseudoanthidium melanurum
Pseudoanthidium rhombiferum
Pseudoanthidium alpinum
Pseudoanthidium lituratum
Pseudoanthidium ochrognathum
Anthidium pulchellum
Anthidium echinatum
Anthidium anguliventre
Anthidium rotundum
Anthidium undulatiforme
Anthidium undulatum
Anthidium oblongatum
Anthidium gussakovskiji
Anthidium tesselatum
Anthidium wüstneii
Anthidium waltlii
Anthidium caspicum
Anthidium diadema
Anthidium spiniventre
Anthidium luctuosum
Anthidium trispinosum
Anthidium auritum
Anthidium punctatum
Anthidium montanum
Anthidium pullatum
Anthidium cingulatum
Anthidium loti
Anthidium taeniatum
Anthidium dalmaticum
Anthidium manicatum
Anthidium christianseni
Anthidium septemspinosum
Anthidium florentinum


Pseudoanthidium melanurum
Pseudoanthidium rhombiferum
Pseudoanthidium alpinum
Pseudoanthidium lituratum
Pseudoanthidium ochrognathum
Anthidium pulchellum
Anthidium echinatum
Anthidium anguliventre
Anthidium rotundum
Anthidium undulatiforme
Anthidium undulatum
Anthidium oblongatum
Anthidium gussakovskiji
Anthidium tesselatum
Anthidium wüstneii
Anthidium waltlii
Anthidium caspicum
Anthidium diadema
Anthidium spiniventre
Anthidium luctuosum
Anthidium trispinosum
Anthidium auritum
Anthidium punctatum
Anthidium montanum
Anthidium pullatum
Anthidium cingulatum
Anthidium loti
Anthidium taeniatum
Anthidium dalmaticum
Anthidium manicatum
Anthidium christianseni
Anthidium septemspinosum
Anthidium florentinum

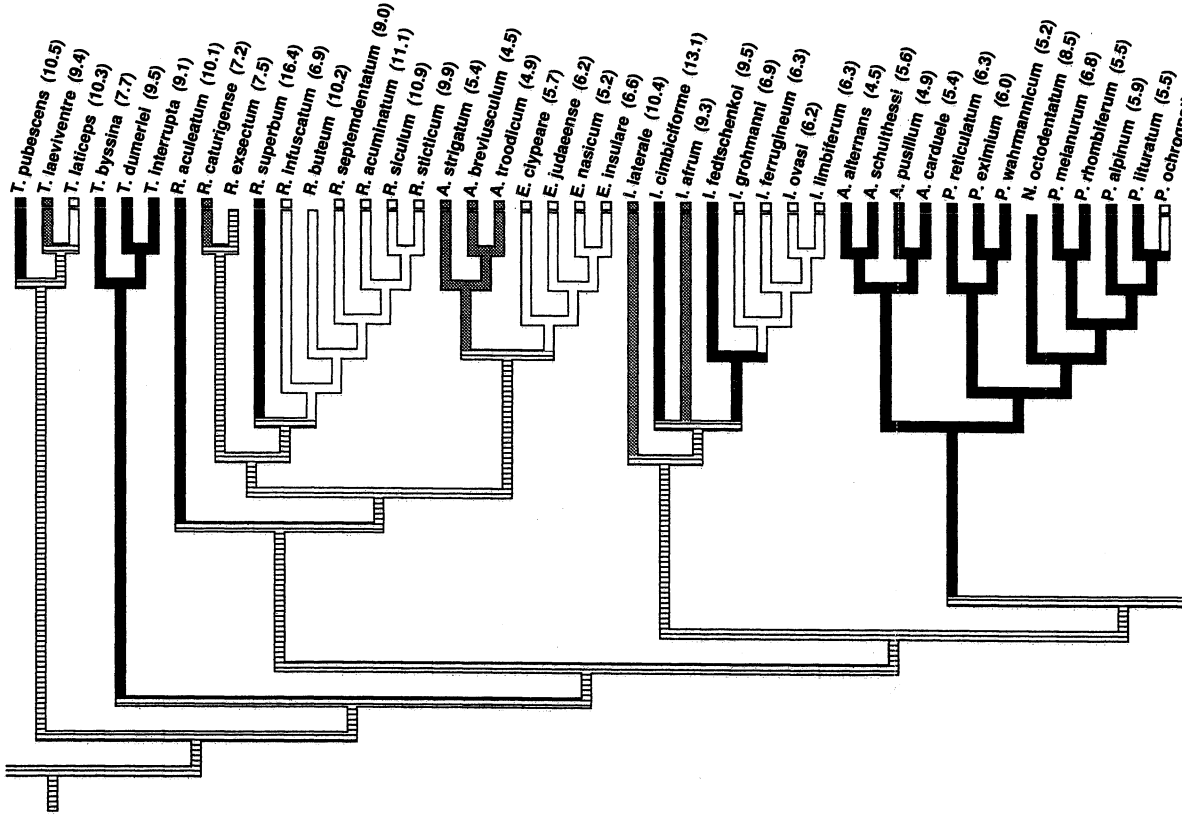
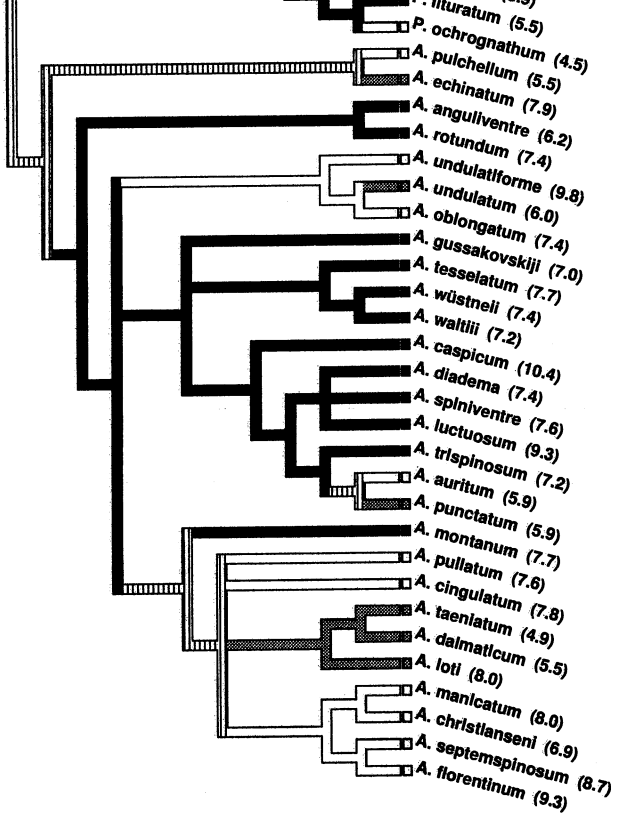


FIG. 3. Host-plant preferences mapped onto the semistrict consensus tree of 72 most parsimonious cladograms. Black: oligolectic; gray: polylectic with strong preference for one plant family; white: polylectic; hatched: equivocal. The ingroup node was forced to be equivocal regarding the three classes of host-plant specialization. For each species, the average length (mm) of forewing of three randomly chosen females is given in parentheses.


P. lituratum (5.5)
P. ochrognathum (4.5)
A. pulchellum (5.5)
A. echinatum (7.9)
A. anguliventre (6.2)
A. rotundum (7.4)
A. undulatiforme (9.8)
A. undulatum (6.0)
A. oblongatum (7.4)
A. gussakovskiji (7.0)
A. tesselatum (7.7)
A. wüstneli (7.4)
A. waltlii (7.2)
A. caspicum (10.4)
A. diadema (7.4)
A. spiniventre (7.6)
A. luctuosum (9.3)
A. trispinosum (7.2)
A. auritum (5.9)
A. punctatum (5.9)
A. montanum (7.7)
A. pullatum (7.6)
A. cingulatum (7.8)
A. taeniatum (4.9)
A. dalmaticum (5.5)
A. lotti (8.0)
A. manicatum (8.0)
A. christianseni (6.9)
A. septemspinosum (8.7)
A. florentinum (9.3)

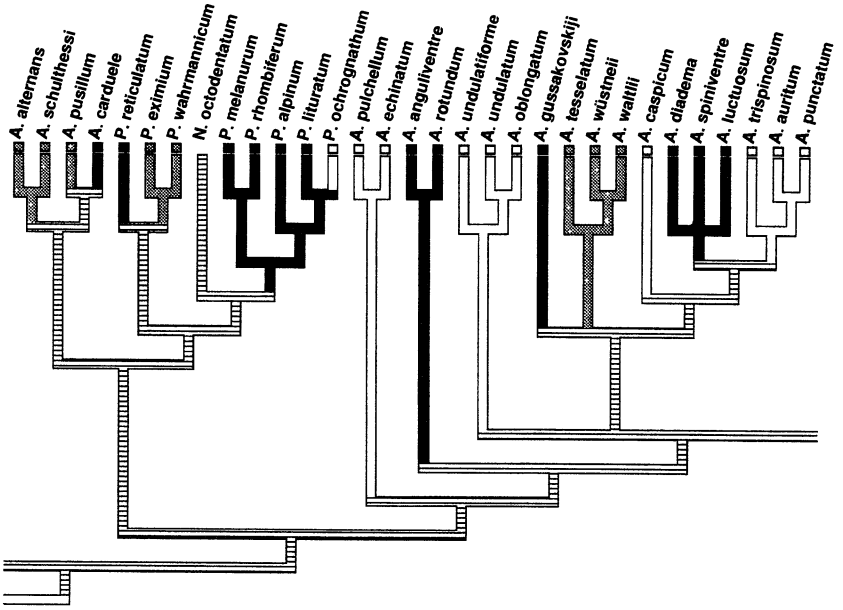


FIG. 4. Host-plant preferences mapped onto the semistrict consensus tree of 72 most parsimonious cladograms. Black: oligolectic on Cardueae (Compositae); gray: oligolectic on Asteroideae (Compositae); white: polylectic or oligolectic on other plant taxa than Compositae; hatched: equivocal. Only a section of the tree is shown.

len of the Cruciferae was detected in the 17 pollen samples of *A. echinatum.* Whether this species actually restricts its pollen harvesting to the Zygophyllaceae and the Cruciferae or whether only flowers of these two families are available in the desert habitats of this spring bee is an open question. Cardueae (Compositae) are the exclusive pollen sources of both *A. anguliventre* and *A. rotundum. A. undulatiforme, A. undulatum,* and *A. oblongatum* are all polylectic harvesting pollen on up to eight families. *A. undulatum* exhibits a distinct preference for Leguminosae whereas *A. undulatiforme* may possibly show a predilection for Labiatae. However, the small number of investigated samples renders this conclusion for the latter species uncertain.

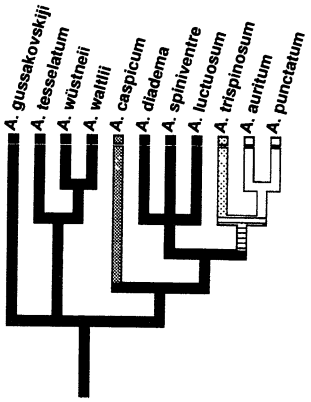


FIG. 5. Host-plant preferences mapped onto the semistrict consensus tree of 72 most parsimonious cladograms. Black: oligolectic on Compositae (either Cardueae or Asteroideae); gray: oligolectic on Campanulaceae; stippled: oligolectic on Leguminosae; white: polylectic; hatched: equivocal. Only a section of the tree is shown.

The following clade contains mainly oligolectic species. *A. gussakovskiji, A. diadema, A. spiniventre,* and *A. luctuosum* exclusively visit Cardueae (Compositae) for pollen. *A. tesselatum, A. wüstneii,* and *A. waltlii* are oligolectic on Compositae as well but they restrict pollen foraging to the disk-shaped flower heads of the subfamily Asteroideae. They possess a specialized pilosity on the ventral side of the thorax which probably evolved to brush pollen from the flat composite inflorescences (see *Results: Specialized morphological structures*). *A. caspicum* and *A. trispinosum* are most probably oligoleges of Campanulaceae and Leguminosae, respectively. *A. auritum* and *A. punctatum* are polylectic visiting up to nine plant families, the latter additionally shows a distinct preference for Leguminosae. A well-substantiated transition from oligolecty to polylecty occurred between the ancestor of the clade *A. trispinosum, A. auritum,* and *A. punctatum* and the common ancestor of *A. auritum* and *A. punctatum.* In addition, several switches of oligolectic species between different plant taxa are inferred from the estimated phylogeny of this clade: one or two transitions within the Compositae, a transition from Compositae to Campanulaceae, and a change from Compositae to Leguminosae (Figs. 4 and 5).

A. montanum is oligolectic on Leguminosae. The other species of this clade are polylectic to a greater or lesser degree. For most of them, Leguminosae are also important pollen sources. In addition, they collect pollen to differing but mostly considerable degrees on

Labiatae and Scrophulariaceae. For harvesting pollen from the raised anthers of flowers of these two families, they are equipped with a specialized pollen-collecting apparatus on the face (see *Results: Specialized morphological structures*). *A. loti, A. taeniatum, A. dalmaticum,* and *A. manicatum* largely restrict their pollen-harvesting efforts to the Leguminosae, Labiatae, and Scrophulariaceae. *A. loti* and *A. taeniatum* additionally exhibit a strong preference for Leguminosae, and *A. dalmaticum,* which is partially sympatric with its closest relative, *A. taeniatum,* predominantly exploits Labiatae. Flowers of the Leguminosae, Labiatae, Scrophulariaceae, and Compositae are the preferred pollen sources of *A. cingulatum.* Both *A. septemspinosum* and *A. florentinum* differ from the other species of this clade in that they show a higher degree of polylecty. They frequently collect pollen on *Rubus* (Rosaceae). No decision on the ancestral state of this monophyletic group is possible, a transition from oligolecty to polylecty is equally parsimonious as the reverse.

In summary, based on the estimated phylogeny (Fig. 2) and the assumption of parsimony, several transitions from oligolecty to polylecty and of oligoleges between different plant taxa appear to have occurred within the anthidiine clades. Two changes from oligolecty to polylecty are well substantiated, two further are most probable. The direction of two other transitions is unknown. At least eight within-clade switches of oligolectic species between different plant taxa were recorded. I found no transition from a polylectic to an oligolectic habit. This holds true as well if between-clade switches are considered. Inspection of the basal conjunctions of the phylogenetic tree reveals that the ancestral nodes are mostly equivocal regarding the degree of host-plant specialization (Fig. 3). However, two basal ancestors within the genus *Anthidium* are assumed to have been oligolectic (Fig. 3) inferring again a switch from oligolecty to polylecty in the precursors of the clade *A. undulatiforme, A. undulatum,* and *A. oblongatum.* Resolving the tritomy in each of the three possible ways always supports this direction of change. If the ancestor of the investigated anthidiine bees was oligolectic, the present distribution of oligolectic and polylectic species in the western palearctic Anthidiini can be explained solely by transitions from the oligolectic to the polylectic habit and by shifts of oligoleges between different plant taxa.

Three of the four transitions from oligolecty to polylecty assumed to have occurred within the clades of the anthidiine species are accompanied by a reduction in bee body size (Fig. 3). The *Icteranthidium* species found to be polylectic are distinctly smaller than the remaining bees of this genus which all exhibit an exclusive or nearly exclusive predilection for the flowers of the Cardueae (Compositae). *P. ochrognathum,* the sole polylectic representative of the genus *Pseudoanthidium,* is the smallest species within this clade. *A. auritum* and *A. punctatum,* both polylectic, are of a distinctly smaller body size than their near relatives which are all oligolectic. In *Rhodanthidium,* no clear statement on any change in body size with respect to the supposed switch from oligolecty to polylecty can be made. *R. superbum,* the oligolectic sister of the polylectic species of *Rhodanthidium* s. str., is by far the largest bee in this group. *R. caturigense* and *R. exsectum,* however, of which at least the former is almost oligolectic, are of about equal size or even smaller than the polylectic *Rhodanthidium* species.

Short-term specialization of individual bees

On average, I recorded pollen grains of 1.4 plant species in the loads of oligolectic species in contrast to 2.2 plant species found in the samples of polyleges (Table 3). The mean number of plant species exploited by polylectic species exhibiting a strong preference for a single plant family was 1.8. *R. exsectum, R. buteum,* and *N. octodentatum* were excluded from the comparison because of the low number of samples available. Comparing only scopae that were filled to the same amount, the mean number of plant species visited during a foraging bout always proved to be lowest in the oligoleges and highest in the polyleges. The species with a strong preference for one plant family occupy an intermediate position (Table 3). The frequency distribution of the number of plant species per scopal load (Table 3) of oligoleges and the frequency distributions added up for both classes of polyleges proved to be significantly different independent of the size of the scopal pollen amounts (chi-square test, $P < 0.001$). Thus, on average, the polylectic anthidiine bees visit more plant species for pollen uptake during a single foraging bout than the oligolectic species.

Specialized morphological structures

Clypeus with wavy hairs.—The clypeus in the females of the following nine *Anthidium* species is densely covered with peculiar hairs that are thickened at their base and extended into a thin, wavy tail (Fig. 6A,B): *A. pullatum, A. cingulatum, A. loti, A. taeniatum, A. dalmaticum, A. manicatum, A. christianseni, A. septemspinosum,* and *A. florentinum.* In the smaller species *A. taeniatum, A. dalmaticum,* and *A. christianseni,* the supraclypeal area is additionally covered with such hairs. This special facial pilosity is absent in the males. As was recently shown (A. Müller, *in press a*), this pilosity is an adaptation for pollen uptake from flowers of Labiatae and Scrophulariaceae where the stamens are placed in such a manner that they come into contact with the dorsal surface of the forager's body ("nototribic"). Nototribic flowers are worked by the pollen-collecting females by rubbing the facial area covered with the transformed hairs repeatedly over the raised anthers with rapid back and forth movements picking up the pollen grains directly into the specialized pilosity (see Table 4). The importance of pollen from

TABLE 3. Frequency distribution of the number of plant species recorded in the anthidiine pollen loads. For comparing frequency distributions of oligoleges and polyleges, polylectic classes were summed.

Pollen load	Number of plant species recorded in the examined loads	Oligolectic (N = 31 species)	Polylectic with a strong preference for one plant family (N = 13 species)	Polylectic (N = 25 species)
Scopa filled to 1/5		n = 94	n = 43	n = 73
		mean* = 1.60	mean = 1.98	mean = 2.26
	1	52	13	18
	2	30	20	30
	3	10	8	15
	4	2	2	8
	5	0	0	2
Scopa filled to 2/5		n = 170	n = 119	n = 165
		mean = 1.36	mean = 1.92	mean = 2.22
	1	119	53	50
	2	42	34	57
	3	9	23	37
	4	0	7	17
	5	0	2	2
	6	0	0	1
	7	0	0	1
Scopa filled to 3/5		n = 173	n = 128	n = 183
		mean = 1.34	mean = 1.83	mean = 2.28
	1	128	61	53
	2	34	40	67
	3	9	18	39
	4	2	7	14
	5	0	1	4
	6	0	1	5
	7	0	0	1
Scopa filled to 4/5		n = 141	n = 81	n = 107
		mean = 1.34	mean = 1.81	mean = 2.07
	1	94	32	43
	2	39	38	34
	3	7	7	18
	4	1	2	8
	5	0	2	1
	6	0	0	2
	7	0	0	1
Scopa filled to 5/5		n = 113	n = 66	n = 99
		mean = 1.35	mean = 1.53	mean = 2.04
	1	80	39	35
	2	27	20	42
	3	6	6	12
	4	0	1	6
	5	0	0	2
	6	0	0	1
	7	0	0	1
Total		n = 691	n = 437	n = 627
		mean = 1.39	mean = 1.82	mean = 2.19
	1	473	198	199
	2	172	152	230
	3	41	62	121
	4	5	19	53
	5	0	5	11
	6	0	1	9
	7	0	0	4

* Means represent the mean number of plant species visited during a single foraging bout.

Labiatae and Scrophulariaceae for the larval nourishment of the species mentioned above is shown in Table 2. It is interesting to note that none of them is completely dependent on the pollen of nototribic flowers, all are polylectic to a higher or lesser degree.

The nine species equipped with this specialized pollen-collecting apparatus constitute a monophyletic group. A cladistic analysis run without the character "female clypeus with wavy hairs for pollen uptake" (character number 6 in Appendix 1) to prevent circularity resulted in no change in the topology of the most parsimonious trees (Fig. 7). The development of the

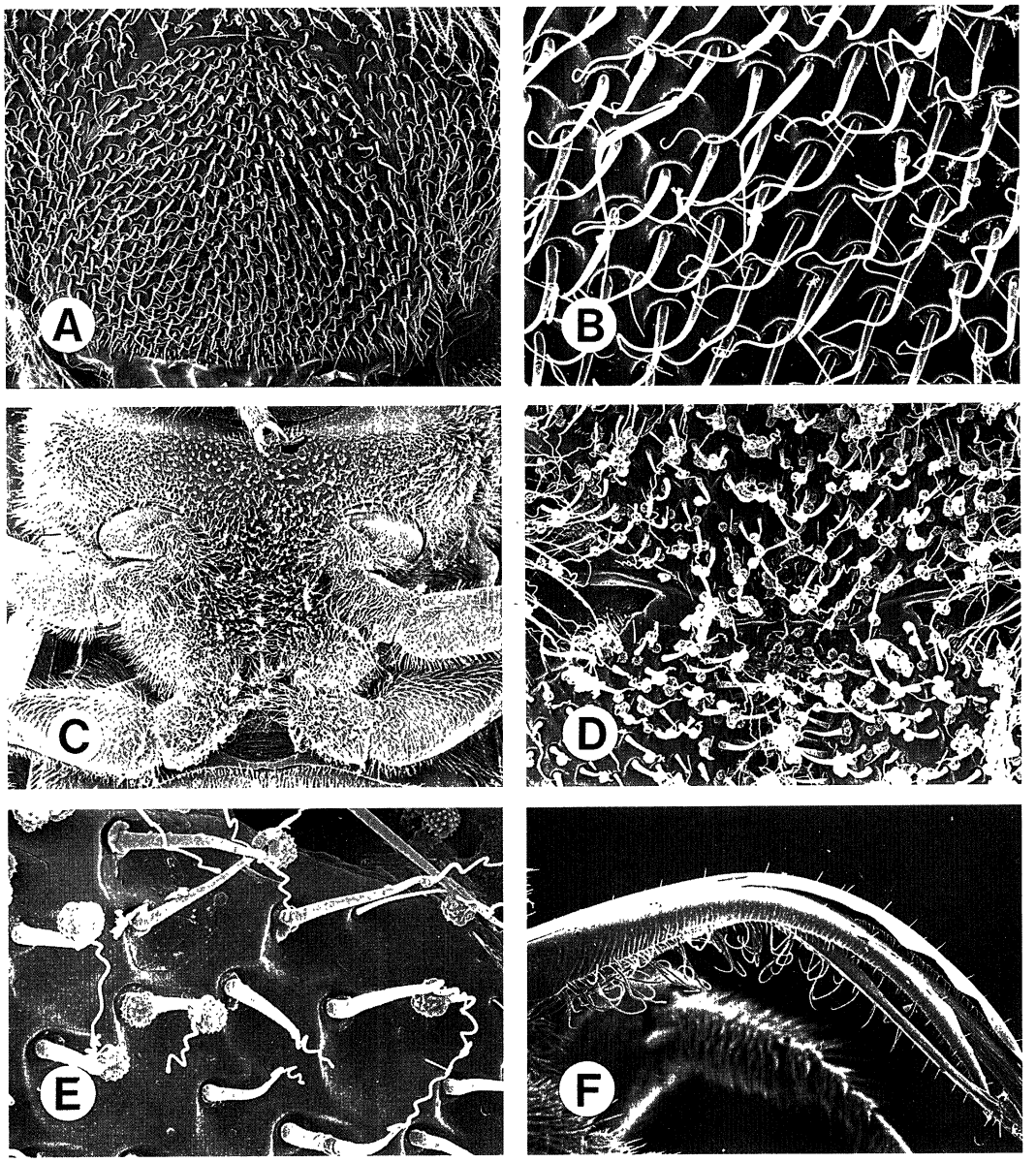


FIG. 6. (A, B) Specialized facial pilosity of *Anthidium manicatum*: Clypeus (35× and 130×). (C, D, E) Specialized pilosity on the ventral side of the thorax of *Anthidium wüstneii*. Ventral side of thorax (13×, 60×, and 200×). (F) Hooked bristles on the labial palpi of *Anthidiellum breviusculum* (45×).

specialized facial pilosity is thus assumed to have occurred only once in the evolutionary history of these *Anthidium* bees.

Other anthidiine species that lack any obvious morphological adaptations also harvest pollen from nototribic flowers. *T. pubescens, R. aculeatum, A. breviusculum, A. troodicum,* and others are heavily dependent on flowers of Labiatae (Table 2). It is assumed, however, that these species use specialized behaviors to extract pollen from the raised anthers of nototribic flowers (A. Müller, *in press a*).

Ventral side of thorax with corkscrew-like hairs.—In the females of *A. tesselatum, A. waltlii,* and *A. wüstneii,* the ventral side of the thorax and the coxae and trochanters of the mid and hind legs are covered with numerous corkscrew-like hairs robust at their base and helically twisted in their apical portion (Fig. 6C,D,E). Similar hairs are lacking in the males.

The three species collect pollen exclusively on Compositae (Table 2). All pollen grains examined belonged to the *Aster* type (Moore et al. 1991) typical of the composite tribes Inuleae, Gnaphalieae, Calenduleae, Astereae, Senecioneae, Heliantheae, and Eupatorieae. These tribes are characterized by having numerous

TABLE 4. Organs involved in pollen uptake from the flowers of different plant species in 14 anthidiine bees. I, II, III = fore, middle, hind legs; S = metasomal scopa; C = specialized pilosity of the clypeus; M = mandibles; I_p, II_p = predominantly with fore, middle legs; ( ) = observed only in rare cases. For degree of specialization, 1 = oligolectic; 2 = polylectic with a strong preference for one plant family; 3 = polylectic.

Bee species	Degree of specialization	Plant species	Organs used for pollen uptake from the anthers or the pollen-bearing flower structures	Observation localities
Trachusa byssina	1	*Lotus corniculatus* (Leguminosae)	III	Merishausen (Schaffhausen), Switzerland
Trachusa interrupta	1	*Scabiosa triandra* (Dipsacaceae)	I_p + II	Euseigne (Valais), Switzerland
Rhodanthidium caturigense	2	*Ononis natrix* (Leguminosae)	III	Zeneggen (Valais), Switzerland
Anthidiellum strigatum	2	*Lotus corniculatus* (Leguminosae)	S	Andelfingen (Zürich), Switzerland
		Linaria vulgaris (Scrophulariaceae)	I	Mt. St. Angelo (Puglia), Italy
Icteranthidium laterale	2	*Centaurea vallesiaca* (Cardueae, Compositae)	S	Susten (Valais), Switzerland
Pseudoanthidium melanurum	1	*Centaurea vallesiaca* (Cardueae, Compositae)	S	St. Christophe (Aosta), Italy
Pseudoanthidium lituratum	1	*Centaurea vallesiaca* (Cardueae, Compositae)	S	Susten (Valais), Switzerland
Pseudoanthidium reticulatum	1	*Centaurea alba* (Cardueae, Compositae)	S	Mt. St. Angelo (Puglia), Italy
Pseudoanthidium eximium	1	*Pulicaria dysenterica* (Asteroideae, Compositae)	S	St. Christophe (Aosta), Italy
Anthidium oblongatum	3	*Sedum album* (Crassulaceae)	I + II_p	Zürich (Zürich), Switzerland
		Onobrychis viciifolia (Leguminosae)	III (II + III)	Zürich (Zürich), Switzerland
		Lotus corniculatus (Leguminosae)	III (II + III)	Merishausen (Schaffhausen), Switzerland
Anthidium punctatum	2	*Lotus corniculatus* (Leguminosae)	III	Merishausen (Schaffhausen), Switzerland
Anthidium cingulatum	3	*Stachys cretica* (Labiatae)	C	S. Giovanni (Puglia), Italy
Anthidium manicatum	3	*Ononis arvensis* (Leguminosae)	III	Westerkamp (1987)
		Ononis spinosa (Leguminosae)	III	Westerkamp (1987)
		Calamintha nepeta (Labiatae)	C	Ruggiano (Puglia), Italy
		Stachys cretica (Labiatae)	C	Mt. St. Angelo (Puglia), Italy
		Stachys recta (Labiatae)	C	Zürich (Zürich), Switzerland
		Teucrium scorodonia (Labiatae)	C	Zürich (Zürich), Switzerland
		Antirrhinum majus (Scrophulariaceae)	C	Zürich (Zürich), Switzerland
		Digitalis lanata (Scrophulariaceae)	C	Zürich (Zürich), Switzerland
		Digitalis purpurea (Scrophulariaceae)	I (I + M)	Zürich (Zürich), Switzerland
		Linaria genistifolia (Scrophulariaceae)	C	Zürich (Zürich), Switzerland
		Misopates orontium (Scrophulariaceae)	C	Zürich (Zürich), Switzerland
Anthidium florentinum	3	*Rubus* species (Rosaceae)	I + II_p	Manfredonia (Puglia), Italy

flowers densely packed in a single plane within an inflorescence all offering pollen at the same height. It is likely that female bees harvest pollen by crawling across the flower heads, pressing the ventral side of the thorax against the pollen-bearing structures, and thereby brushing the pollen grains into the specialized pilosity. Females of *Pseudoanthidium eximium,* which mainly restrict pollen collecting to the same kind of composite floral heads (Table 2), harvest pollen by rapidly seesawing their scopal brush against the surface of the flat composite inflorescences (see Table 4). Compared to *P. eximium* (average length of forewing: 6.1 mm), however, the three *Anthidium* species are distinctly larger (average length of forewing: 7.2, 7.4, and 7.7 mm). The composite flower heads are frequently small, probably rendering the uptake of pollen with the metasomal scopa more difficult for larger bees. Selection might thus have favored the development of specialized hairs on the ventral side of the thorax in the three *Anthidium* species instead.

The three *Anthidium* species are closely related. Excluding the character "ventral side of female thorax with corkscrew-like hairs for pollen uptake" (character number 17 in Appendix 1) from the cladistic analysis maintains their monophyly (Fig. 7).

Mouthparts with hooked bristles.—The two basal segments of the labial palpi of the females of *Anthidiellum breviusculum* are provided with long, hooked bristles (Fig. 6F) not present in the males. Hooked bristles on the proboscis, around the proboscidial fossa, or

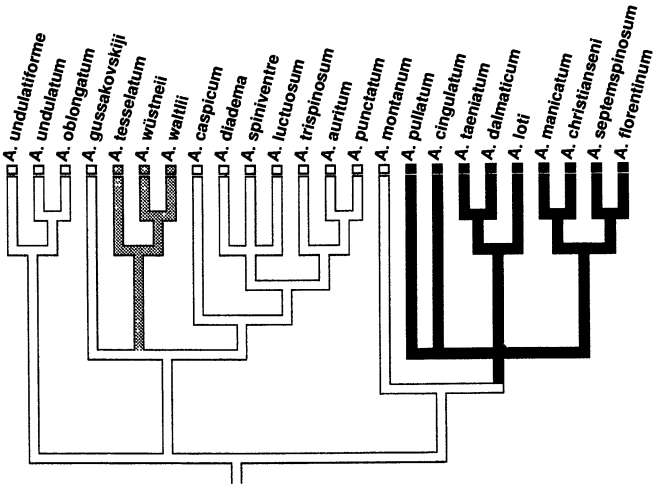


FIG. 7. Specialized pollen-harvesting structures mapped onto the semistrict consensus tree of 72 most parsimonious cladograms. Black: specialized facial pilosity for removing pollen from nototribic flowers; gray: specialized pilosity of ventral side of thorax which presumably evolved for harvesting pollen from disk-shaped Compositae. Only a section of the tree is shown. Characters 6 and 17 (see Appendix 1) were excluded from the analysis.

on the forelegs are known to have evolved in many bees for scraping pollen out of flowers that have their anthers enclosed in narrow tubes, viz. Boraginaceae, Primulaceae, and others (Peters 1974, Thorp 1979, Parker and Tepedino 1982; A. Müller, *in press b*). *A. breviusculum,* however, shows a strong preference for the pollen of Labiatae, no pollen grains of narrow-tubed flowers were detected in the pollen loads examined (Table 2). The function of the hooked bristles on the proboscis of *A. breviusculum* which are lacking in its nearest relatives *A. troodicum* and *A. strigatum* remains enigmatic. It seems improbable that the occurrence of hooked bristles is connected with pollen harvesting in any way since *A. troodicum* visits essentially the same spectrum of plants for pollen as *A. breviusculum* (Table 2).

In general, pollen from narrow-tubed flowers plays a negligible role in the larval nourishment of the western palearctic anthidiine species. Pollen grains of Primulaceae and of the tribe Boragineae of the Boraginaceae, which represent that flower type, were rarely detected in pollen loads and then only in small quantities (Table 2). This supports the supposition that bee species lacking specialized morphological devices are unable to harvest pollen from anthers concealed within narrow flower tubes in an efficient manner (A. Müller, *in press b*).

Pollen-harvesting behavior

The pollen-harvesting behavior of 14 anthidiine bees at the flowers of different plant species was recorded. The organs responsible for removing pollen from the anthers or the pollen-bearing flower structures are listed in Table 4. Several females of each species were observed at the flowers of the same plant species. They worked the flowers in exactly the same manner. Therefore, the methods of pollen uptake from a given plant species seem to be fixed at the bee species level.

When harvesting pollen from the papilionaceous flowers of the Leguminosae, *T. byssina* (oligolectic), *R. caturigense, A. oblongatum, A. punctatum,* and *A. manicatum* (all polylectic) remove the pollen from the tip of the keel with their hind legs before depositing it into the metasomal scopa. The middle legs press the floral wings or the keel down in order to cause the anthers or the pollen grains to protrude. In contrast to the foregoing species, *A. strigatum* (polylectic) embraces the keel of the flowers of *Lotus corniculatus* below its tip with the hind legs. These rhythmically pull the keel down pumping the pollen out of the aperture at the tip of the keel. The protruding pollen is then directly picked up into the scopa by repeatedly moving the metasoma up and down.

I. laterale (polylectic), *P. melanurum, P. lituratum,* and *P. reticulatum* (all oligolectic) use their metasomal scopa for the uptake of pollen from the flower heads of *Centaurea.* The hind legs embrace several flowers and guide them under the metasoma while the latter is permanently performing rapid up and down movements, thereby bringing the scopal hairs in contact with the pollen that sticks to the styles. Similarly, *P. eximium* (oligolectic) harvests pollen from the flat, disk-shaped flower heads of *Pulicaria dysenterica* by rapidly seesawing its metasomal scopa against the flowers. The hind legs are not involved in the process of pollen uptake.

A. cingulatum and *A. manicatum* (both polylectic) have evolved a pollen-harvesting apparatus on the clypeus consisting of specialized, wavy hairs (see *Results: Specialized morphological structures*). It is employed for brushing the pollen out of the raised anthers of nototribic flowers. *A. manicatum* is not able, however, to use this specialized tool to remove pollen from the nototribic flowers of *Digitalis purpurea.* Since the flower diameter is too large in this species compared to the size of the bee, the raised anthers are not within reach of the clypeal pilosity. Pollen-collecting females climb the filaments up to the anthers instead and harvest pollen with the forelegs while hanging below the anthers. Occasionally, the mandibles are used to scrape

pollen out of undehisced anthers. *A. strigatum* (polylectic), which lacks a similar morphological device for pollen uptake, forcefully opens the nototribic mask-flowers of *Linaria vulgaris* with its body and legs before removing the pollen from the raised anthers with the forelegs.

The flowers of *Scabiosa, Sedum,* and *Rubus* are characterized by free-standing stamens which are arranged around the flower center. *T. interrupta* (oligolectic), *A. oblongatum,* and *A. florentinum* (both polylectic) gather pollen from the anthers of these flowers by rapid up and down brushing movements of the fore and middle legs while standing on the flowers and turning slowly around their own body axis.

In summary, the methods of pollen uptake proved to be very similar when considering anthidiine bees of different taxonomic groups harvesting pollen at the same type of flowers, viz. Leguminosae, Compositae, or open flowers with free-standing stamens. Although the examples are few, oligolectic species did not distinctly differ from polylectic species in how they remove pollen from the flowers of a given structure. On the other hand, polylectic species exhibited intraspecific flexibility regarding the organs used for pollen uptake from flowers of a different architecture. Depending on the plant species, *A. strigatum* employed the metasomal scopa or the forelegs, *A. oblongatum* the fore and middle or the hind legs, and *A. manicatum* the hind legs, the specialized facial pilosity, or the forelegs for removing pollen from the flowers.

Discussion

Host-plant specializations

In contrast to Pasteels (1977) and Grigarick and Stange (1968) who assumed that Old World Anthidiini and California Anthidiini, respectively, are largely polylectic, a high percentage of the anthidiine species of Europe, North Africa, and Asia Minor exhibit floral specificity. Fox and Morrow (1981) pointed out that feeding specializations in herbivorous insects are often a flexible attribute of a population rather than an attribute of a species throughout its geographic range. However, the microscopic examination of pollen loads originating from many different geographic localities revealed that the oligolectic habit in the anthidiine bees is not a local phenomenon but a species property. Likewise, Dyer and Shinn (1978) and Westrich and Schmidt (1987), who sampled pollen loads of solitary bees across their entire ranges, showed that oligolectic or nearly oligolectic species are faithful to the same host-plants throughout their distribution areas.

The anthidiine bees found to be oligolectic are specific at the level of plant tribe, subfamily, or family. Floral specificity at a lower level could not be detected. In general, the oligolectic habit in bees ranges from restriction to one section of a plant genus to restriction to an entire family (Linsley 1958, Linsley and MacSwain 1958, Linsley et al. 1963, 1964, 1973, Hurd and Linsley 1964, 1975, Stephen et al. 1969, Thorp 1969, Schlising 1972, MacSwain et al. 1973, Moldenke 1976, 1979*a, b,* Grant and Hurd 1979, Hurd et al. 1980, Whitehead 1984, Westrich 1989, Wittmann et al. 1990, Wcislo and Cane, *in press*). Monolecty, the restriction by a bee to a single plant species for pollen uptake, is known to occur only where there is just one species of the plant genus blooming within the range and flight period of the specialist bee species. Thus, true monolecty exhibited in the presence of more than one species of a plant genus does not seem to occur in bees.

All intergradations exist between oligolecty and polylecty (Michener 1979, Moldenke 1979*a,* Westrich 1989, Wcislo and Cane 1996). Polylectic bee species do not usually harvest pollen from whatever flowers are available (Westrich 1989). On the one hand, local populations of polylectic bees may be faithful to one or a few especially rewarding pollen sources even though there is a considerable variety of plants exploited for pollen when the bee species is examined throughout its range (Stephen et al. 1969, Moldenke 1976, 1979*c,* Eickwort and Ginsberg 1980, Rust 1990). On the other hand, polyleges may show differing degrees of host-plant preferences that are constant throughout the range and thus presumably have a genetic foundation (Tasei 1976, Johnson 1984, Westrich 1989). No attempt has been made here to elucidate such genetically based differences of diet breadth in polyleges, since the assessment of host-plant preferences of a polylectic bee species by examining scopal pollen contents is difficult without the exact knowledge of all flowering plants in the surroundings at the time of capture.

By far the most important pollen sources for the western palearctic anthidiine bees are plants of the families Compositae, Leguminosae, and Labiatae. Whereas the latter two families largely consist of typical bee flowers only rarely visited by other kinds of insects (Faegri and Pijl 1979), the Compositae are exploited by many different insect taxa. Graenicher (1935) stressed the importance of the Compositae for oligolectic bees. He found that more than half of the oligoleges of a local bee fauna were associated with this plant family. Similarly, over one-third of all North American specialist bees are dependent on composite flowers (Moldenke 1979*b*). Apart from their abundance of species and their frequent occurrence in most habitats, the high pollen and nectar rewards yielded by the compound inflorescences of the Compositae over an extended time period may account for their attractiveness to oligolectic bees.

Host-plant specializations in the context of anthidiine phylogeny

It has been a widely accepted assumption that oligolectic bees have evolved from polylectic ancestors (Michener 1954, Linsley 1958, MacSwain et al. 1973,

Iwata 1976, Moldenke 1979*b*, *c*, Hurd et al. 1980). Based on published bee phylogenies, Moldenke (1979*b*) lists 253 instances of host-plant shifts in the evolutionary history of North American bees. He assumes that 200 switches have been from generalist to specialist and that 53 switches have occurred in specialist bees between different plant taxa. He could not find evidence for even a single transition from oligolecty to polylecty. In contrast, Kratochwil (1984, 1991) supposes that the oligolectic habit might be the ancestral state in bees while polylecty rather represents the derived foraging strategy. Similarly, J. H. Cane and G. C. Eickwort (*unpublished manuscript*) conclude on grounds of well-substantiated phylogenies for the basal groups of bees that oligolecty may be primitive in most higher bee taxa. They infer from the restricted host-plant spectra of many basal bee groups that oligolecty is ancestral in the long-tongued bees and perhaps the short-tongued bees as well. They present evidence supporting an oligolectic ancestry in the Megachilinae and the Anthophorinae, and further suggest that polylecty has probably secondarily evolved within the Colletidae, Halictidae, and Andrenidae as well. However, they found oligolecty to have probably evolved from polylecty in a few groups within the Andreninae and Halictinae. Westerkamp (1987) and Westrich (1989) also consider oligolecty, and not polylecty, to be usually the primitive condition in bees. In the present study, I detected four transitions from oligolecty to polylecty and at least eight of oligoleges between different plant taxa, but none from polylecty to oligolecty. This supports Kratochwil (1984, 1991), J. H. Cane and G. C. Eickwort (*unpublished manuscript*), Westerkamp (1987), and Westrich (1989).

Compared to oligolectic bees, polyleges must be capable of exploiting flowers of varying architectures and of digesting pollen of different chemical compositions. Thus, the polylectic habit apparently requires greater mental and metabolic abilities than oligolecty. Consequently, oligolecty in bees might possibly be an evolutionary constraint which has been repeatedly overcome by bees of many taxonomic groups rather than a property selected for under certain environmental conditions. It may be of interest in this context that in the sphecid wasps (Sphecidae), which represent the sister group of the bees (Brothers 1975), most species are specialized hunters restricted to certain arthropod groups (Bohart and Menke 1976, Iwata 1976).

Due to the apparently rare shifts from polylecty to oligolecty, the most important process in producing the present oligolectic bee fauna was probably the splitting of an ancestral polylege into two descendent oligolectic species. Two modes of speciation within oligolectic taxa are discussed in the literature (Linsley and MacSwain 1958, 1959, Linsley 1961, Cruden 1972, Moldenke 1979*c*, Westrich 1989, Wcislo and Cane 1996). Both probably occurred also in the anthidiine bees. In the first, the splitting resulted in two descendent species that presumably evolved in geographic isolation maintaining the same host-plant preferences even after eventually becoming wholly or partially sympatric again. Among the anthidiine species investigated, this mode of speciation is most probably exemplified by the following species groups (host plants in parentheses): *A. alternans* and *A. schulthessi* (Asteroideae, Compositae); *P. eximium* and *P. wahrmannicum* (Asteroideae, Compositae); *P. melanurum, P. rhombiferum, P. alpinum,* and *P. lituratum* (Cardueae, Compositae); *A. anguliventre* and *A. rotundum* (Cardueae, Compositae); *A. tesselatum, A. wüstneii,* and *A. waltlii* (Asteroideae, Compositae); *A. diadema, A. spiniventre,* and *A. luctuosum* (Cardueae, Compositae); and presumably also *R. caturigense, R. exsectum,* and *R. superbum* (Papilionoideae, Leguminosae) and *I. laterale, I. cimbiciforme, I. afrum,* and *I. fedtschenkoi* (Cardueae, Compositae). The second mode involves a change in host plants from ancestral to descendent species after either allopatric, parapatric, or possibly sympatric speciation. At least eight within-clade switches of oligoleges between different plant taxa are indicative of this speciation mode among the anthidiine species examined. Four shifts were between different taxa of the Compositae (Cardueae and Asteroideae, respectively) and four between different plant families (between Compositae and Dipsacaceae, between Leguminosae and either Compositae or Dipsacaceae, from Compositae to Campanulaceae, and from Compositae to Leguminosae).

The analysis of scopal pollen contents revealed two possible cases indicative of niche partitioning with respect to the preferred pollen sources. The three *Anthidiellum* species are very close relatives hardly distinguishable by the naked eye. The two allopatric species *A. breviusculum* and *A. troodicum* exhibit a distinct preference for flowers of the Labiatae, whereas *A. strigatum,* which is sympatric with both the other species, exploits mainly Leguminosae. Similarly, the partially sympatric *A. taeniatum* and *A. dalmaticum,* two very closely related members of the genus *Anthidium,* which only slightly differ morphologically, show strikingly different host-plant preferences. The former predominantly visits Leguminosae while the latter depends heavily on Labiatae.

Three of the four switches from oligolecty to polylecty within the anthidiine clades were found to be accompanied by a reduction in bee body size. It is questionable whether this is causally correlated with the change of the foraging strategy. Nevertheless, it is tempting to assume that the size reduction allowed the bees to exploit floral resources of widely different sizes and architectures, i.e., to become polylectic. It is likewise possible that, after switching to the polylectic habit for unknown reasons, selection for smaller body size took place that resulted in the ability of the bees to visit a yet wider array of flowers. However, smallness and polylecty do not have to be correlated at all as the

occurrence of small oligoleges (e.g., species of *Afranthidium* and *Pseudoanthidium*) and large polyleges (e.g., species of *Rhodanthidium* s. str. and *Anthidium*) indicates.

Short-term specialization of individual bees

On average, the oligolectic anthidiine bees visit fewer plant species for pollen during a single foraging bout than the polylectic species. This finding is not trivial. In the bee group under study, the oligolectic habit is not confined to single plant species but is actually developed on tribe, subfamily, or family level leaving the possibility for oligolectic bees to exploit several related plant species on the same foraging trip. Moreover, short-term specialization of individual bees to one plant species is assumed to have evolved as a strategy that enables the insects to increase their foraging efficiency by reducing time and effort involved in learning to locate new sources and to manipulate diverse floral mechanisms (Darwin 1876, Kugler 1943, Waser 1986). Since polylectic species may have no innate knowledge of how to handle a given flower type, they might be more flower constant than oligolectic species, which in contrast already appear to know the floral architecture of their preferred host plants as unexperienced foragers (Laverty and Plowright 1988). Indeed, oligolectic bees frequently do not discriminate between closely related, co-flowering plants during foraging (Westrich 1989), individuals of polylectic species often exhibit a higher degree of flower constancy compared to oligolectic species (Westerkamp 1987), and honey bees, which are pronouncedly polylectic, are famous for maintaining a strong fidelity to a single plant species during foraging (Free 1963).

Specialized morphological structures

Bees usually gather pollen with the basitarsal brushes of the (fore)legs from the anthers or the pollen-bearing flower structures (Grinfel'd 1962, Michener et al. 1978, Westerkamp 1987, Westrich 1989). Basitarsal brushes are widespread among aculeate Hymenoptera where they primarily serve as a grooming device. In bees, they are additionally employed as pollen-harvesting tools. Basitarsal brushes are thus believed to have been a preadaptation to pollen collection in the precursors of the bees (Grinfel'd 1962, Jander 1976). Apart from leg basitarsal brushes, both mandibles and scopal brushes (particularly the metasomal scopa) are also involved in pollen uptake in many bees (Stephen et al. 1969, Westerkamp 1987, Westrich 1989). They too, however, were not specially developed as pollen-harvesting devices, scopal brushes being primarily pollen transport structures (Westerkamp 1987).

Morphological structures specially evolved for pollen uptake are rarely observed in bees (Thorp 1979, Westerkamp 1987, Westrich 1989, Wcislo and Cane 1996). Since the anthers or the pollen-bearing flower structures have to be placed in a suitable position to contact the incoming insects, pollen, in contrast to nectar, cannot be hidden deep inside the flower. Most probably for that reason, morphological adaptations for extracting nectar are more common (Stephen et al. 1969, Westerkamp 1987). Specialized morphological tools for pollen uptake are expected to have evolved only in bees dependent on flowers that are difficult to exploit for pollen in an efficient manner by the usual methods. Apart from a few particular cases, morphological specializations are known at present to occur in bees exploiting one of the following flower types (A. Müller, *in press b*): (1) Nototribic flowers where the raised position of the anthers renders an efficient collection of pollen difficult; (2) Flowers where the anthers are concealed within narrow tubes; (3) Flowers of small size packed in dense inflorescences where the separate exploitation of each small flower is inefficient. For each of these three flower types, similar morphological harvesting devices have independently evolved in numerous bees of several taxonomic groups (A. Müller, *in press a, b*).

Specialized morphological tools for harvesting pollen from two of the above-mentioned flower types were found in the western palearctic anthidiine bees: two *Anthidium* clades are equipped with a pollen-collecting apparatus used to remove pollen from nototribic flowers and from flat inflorescences of Compositae, respectively. Morphological adaptations for extracting pollen from nototribic flowers developed either on the face or on the dorsal area of the thorax are known from other bees (Westrich 1989, Müller, *in press a*). Among the roughly 540 nonparasitic representatives of the Central European apoid fauna, thirteen species belonging to seven taxonomic groups out of the families Halictidae, Megachilidae, and Anthophoridae possess this kind of pollen-harvesting device. Several megachilid and anthophorid bees occurring in mediterranean Europe and in North, Central, and South America are likewise equipped with a similar structure for pollen uptake, as well as two European representatives of the honey wasps (Vespoidea, Masaridae), another group of pollen-collecting hymenopterans (Schremmer 1959, Müller, *in press a*). Specialized bristles for pollen removal from floral heads of Compositae are also developed on the underside of the metasoma of various *Svastra, Xenoglossodes,* and *Tetralonia* species (all Anthophoridae) (Neff 1984, Westerkamp 1987; A. Müller, *personal observation*). Likewise, several paracolletine bees (Colletidae) which collect pollen on the dense inflorescences of *Prosopis* (Mimosoideae, Leguminosae) are provided with a special metasomal pilosity that probably aids in pollen uptake (Simpson et al. 1977, Neff 1984). The hooked bristles on the proboscis of *Anthidiellum breviusculum* were supposed to be employed at first for scraping pollen out of narrow-tubed flowers. In general, hooked bristles on or near the mouthparts or on the forelegs are indicative of a

preference for pollen from plants with anthers concealed inside corolla tubes (Peters 1974, Thorp 1979, Parker and Tepedino 1982, A. Müller, *in press b*). However, the microscopic analysis of pollen loads of *A. breviusculum* later revealed that its hooked bristles serve another, unknown function. No pollen of plants with narrow corolla tubes was found in the samples examined indicating that the occurrence of hooked bristles is not necessarily connected with pollen removal out of narrow flower tubes in every case.

Pollen-harvesting behavior

The number of bee progeny is directly related to the amount of pollen collected per unit time. Selection is expected therefore to force the female bees to collect pollen in an efficient manner. Indeed, a field observer is struck by the single-mindedness with which pollen-harvesting bees exploit the flowers by directly attacking the pollen-bearing flower structures. Thus, pollen gathering by bees is far from an accidental process as the observation of the pollen-collecting anthidiine females in this study also shows. The basic pollen-foraging patterns of the anthidiine species examined seem to have reached a high degree of efficiency as can be judged from the following findings: (1) The females of a given anthidiine species worked the flowers of a certain plant species in a fixed manner; (2) the organs used for pollen uptake from the same flower type were largely the same among anthidiine bees of different taxonomic groups; and (3) no distinct differences with respect to the basic pattern of pollen removal from flowers of the same architecture were obvious when comparing oligolectic and polylectic species. Similarly, the intraspecific flexibility in polylectic species regarding the organs used to gather pollen from different flower types points to the ability of the bees to increase efficiency by adapting their motor patterns to differing flower architectures.

Strickler (1979) showed that the specialist bee *Hoplitis anthocopoides* forages for pollen from *Echium vulgare,* its preferred host plant, more efficiently than do four generalist bee species. My finding that the few oligolectic anthidiine species examined do not distinctly differ from polylectic species in the manner they remove pollen from the flowers does not contradict Strickler's results. The higher efficiency of *H. anthocopoides* was found to be the result of a shorter handling time per flower, an ability to remove pollen from more anthers per flower on average, and a shorter time spent in flight between flowers, but not of the basic foraging pattern that was observed to be actually the same in both *H. anthocopoides* and the generalist megachilids.

Acknowledgments

The following persons generously allowed me to remove pollen samples from anthidiine bees of their private collections: F. Amiet, M. Bernasconi, S. Blank, F. Brechtel, D. Doczkal, A. W. Ebmer, J. Gusenleitner, M. Hauser, G. Jaeschke, W. Linsenmaier, H. Özbek, T. Petanidou, S. Risch, C. Schmid-Egger, M. Schwarz, E. Steinmann, B. Tkalcu, the late K. Warncke, P. Westrich, H. Wiering, and G. van der Zanden.

The conservators of the entomological collections of the institutions mentioned below kindly permitted the collection of pollen samples as well: Eidgenössische Technische Hochschule Zürich, Naturhistorisches Museum Bern, Muséum d'Histoire Naturelle Genève, Musée Zoologique Lausanne, Bündner Naturmuseum Chur, Zoologische Staatssammlung München, Forschungsinstitut und Naturmuseum Senckenberg Frankfurt, Deutsches Entomologisches Institut Eberswalde, Museum für Naturkunde der Humboldt-Universität Berlin, Oberösterreichisches Landesmuseum Linz, Naturhistorisches Museum Wien, The Natural History Museum London, Liverpool Museum, Nationaal Natuurhistorisch Museum Leiden, Zoölogisch Museum Amsterdam, Zoologisk Museum Copenhagen, Zoological Museum Helsinki, Institut Royal des Sciences Naturelles de Belgique Bruxelles, Muséum National d'Histoire Naturelle Paris, Museo Nacional de Ciencias Naturales Madrid, Estación Biológica de Doñana, Zoological Institute St. Petersburg, and Tel Aviv University.

M. Schwarz, the late K. Warncke and the conservators of the entomological collections of the Eidgenössische Technische Hochschule Zürich, Forschungsinstitut und Naturmuseum Senckenberg Frankfurt, Museum für Naturkunde der Humboldt-Universität Berlin and Muséum National d'Histoire Naturelle Paris sent anthidiine specimens for the cladistic analysis on loan.

For guidance, advice, assistance and comments I thank P. K. Endress, the late K. U. Kramer, R. Wehner, P. Westrich, C. Westerkamp, F. Amiet, the late K. Warncke, D. Agosti, J. Plant, R. W. Brooks, L. Wick, J. H. Cane, R. Holderegger, A. McNeil, U. Jauch, and A. Zuppiger.

Detailed comments of N. M. Waser and two anonymous reviewers substantially improved the manuscript.

Financial support for the printing of the foldouts was received from the Claraz Foundation.

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APPENDIX 1

Character and character states used in the cladistic analysis of the anthidiine bees. If not otherwise stated, the characters refer to both sexes. The terminology of bee morphology follows Michener et al. (1994).

1) Number of segments of maxillary palpi: 2 (2); 3–4 (1); 5 (0).

Pasteels (1969) and Warncke (1980) mention the occurrence of five-segmented maxillary palpi in T. byssina. *By examining several specimens of this species applying scanning electron microscopy, the maxillary palpi were found to be composed of four segments only. Griswold & Michener (1988) also point out that* T. byssina *possesses four-segmented maxillary palpi.*

2) Attachment of the third segment of the labial palpi to the second segment: laterally (1); apically (0).

3) Labrum with two subbasal tubercles with a shiny and deepened, longitudinal area in between (1); without tubercles (0).

4) Number of mandibular teeth: 8–11 (2); 5–6 (1); 3–4 (0).

5) Clypeus and/or area between compound eyes and clypeus with yellow maculations in males (1); without yellow maculations (0).

6) Female clypeus with wavy hairs for pollen uptake (1); without wavy hairs (0).

7) Apical margin of female clypeus with tooth medially (1); without tooth (0).

8) Female clypeus with distinctly bordered apical margin which is thrown up to a lesser or higher degree and mostly denticulate (1); female clypeus of different shape (0).

9) Epistomal suture of male distinctly to slightly curved (1); more or less straight (0).

10) Subantennal suture very strongly curved (1); straight or slightly curved (0).

11) Inner margins of the antennal sockets distinctly carinate (2); slightly carinate (1); not carinate (0).

12) Antennal segments 8–11 of female distinctly to slightly wider than long (1); longer than wide or as long as wide (0).

13) Compound eyes of female unusually large (1); normally sized (0).

14) Preoccipital ridge distinctly keeled from above up to the base of the mandible (1); not keeled (0).

15) Preoccipital ridge keeled above (1); keel absent or if present also developed below up to the base of the mandible (0).

16) Pilosity of vertex and dorsal area of thorax brightly fox-colored conspicuously contrasting with the white-haired face and thorax sides (1); differently colored (0).

17) Ventral side of female thorax with corkscrew-like hairs for pollen uptake (1); without wavy hairs (0).

18) Arolia absent (1); present (0).

19) Tarsal claws of female cleft (1); not cleft (0).

20) Basitarsi 1–2 of female with dense, white pubescence of fine, multiple-branched hairs (1); normally haired (0).

In A. florentinum *and* A. septemspinosum, *this basitarsal pubescence is not as distinctly developed as in the other species.*

21) Basitarsus 3 of female slender, more than three times longer than wide (1); basitarsus broader, less than or equal to three times longer than wide (0).

22) Tibia 3 of female keeled (1); not keeled (0).

23) Distal process of tibia 1 a triangular and pointed tooth (1); rounded, emarginated or a curved spine (0).

24) Distal process of tibia 1 and 2 of female deeply emarginated and two-pronged (1); rounded, pointed or slightly emarginated (0).

25) Femur 1 of male with pointed spine proximally (1); without spine (0).

26) Femur 3 of male with tooth proximally (2); with weak tubercle (1); normally rounded (0).

27) Trochanter 3 of male with long tooth directed towards posterior (3); with short tooth (2); with weak tubercle (1); tooth absent or if present directed towards anterior (0).

28) Trochanter 3 of male with tooth directed towards anterior (1); tooth absent or if present directed towards posterior (0).

29) Insertion of the second recurrent vein of the forewing: beyond the second submarginal cell or interstitial (1); within the second submarginal cell (0).

30) Stigma of forewing short, its inner margin shorter than, equal to, or slightly longer than its maximal width (1); stigma longer (0).

31) Upper margin of propodeum laterally with row of pits and/or posterior margin of propodeal spiracle distinctly carinate (1); without row of pits and margin of spiracle not carinate (0).

32) Triangular area of propodeum large, covering nearly one-half of the posterior surface of the latter (1); smaller, covering about one-third (0).

33) Thorax hemispherical, metanotum surpassed by scutellum (1); metanotum not surpassed by scutellum (0).

34) Female body distinctly globular (1); not distinctly globular (0).

35) Terga with yellow or red maculations (1); without pale maculations (0).

The tergal maculations are reduced to small yellow spots in females of A. pullatum. *In* A. montanum, *there are specimens with small yellow spots on the terga.*

36) Pale maculations of terga of female partially or completely red-colored (1); pale maculations absent or if present all yellow-colored (0).

37) Horizontal portion of tergum 1 of female slightly wider medially than laterally (1); distinctly narrower medially than laterally (0).

38) Anterior portion of tergum 2 of female distinctly impressed (1); not impressed or only slightly so (0).

39) Posterior margin of tergum 2 (and 3) of female with small appendage medially (1); without appendage (0).

40) Posterior margins of terga 3, 4, and 5 of female with conspicuous fringe of white hairs (1); not distinctly fringed or hair fringes developed on other terga (0).

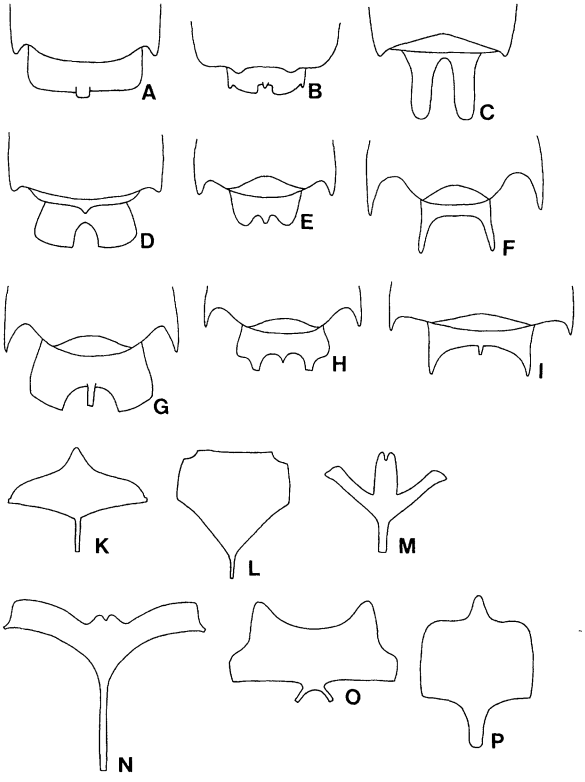

FIG. A1. A–I, shape of tergum 7 of male; K–P, shape of sternum 8 of male. The absence of the letter "J" for labeling is due to the similarity of the pronunciation of "I" and "J" in German.

41) Anterior portion of tergum 5 of female distinctly bulged (1); not bulged or only slightly so (0).

42) Posterior margin of tergum 5 of female slightly curved out or with small appendage medially (1); evenly rounded (0).

43) Posterior margin of tergum 6 of male with two long spines in addition to lateral teeth (2); with two small tubercles (1); without spines or tubercles (0).

44) Posterior margin of tergum 6 of male distinctly denticulated (2); slightly denticulated (1); not denticulated (0).

45) Tergum 6 of male with projecting plate posteriorly (1); without projecting plate (0).

46) Posterior margin of tergum 6 of female with strongly projecting lateral edges resulting in a distinct emargination of tergum 6 (1); tergum 6 of different shape (0).

47) Tergum 6 of female distinctly impressed (1); of different shape (0).

48) Subapical margin of tergum 6 strongly denticulate in both sexes (1); not denticulate, slightly denticulate or denticulate in one sex only (0).

49) Tergum 7 of male with bulging transverse elevation centrally (1); without transverse elevation (0).

50–59) Shape of tergum 7 of male:

50) as in Fig. A1, A (1); of different shape (0).

51) as in Fig. A1, B (1); of different shape (0).

52) as in Fig. A1, C (1); of different shape (0).

53) as in Fig. A1, D (1); of different shape (0).

54) as in Fig. A1, E (1); of different shape (0).

55) as in Fig. A1, F (1); of different shape (0).

56) as in Fig. A1, G (1); of different shape (0).

57) as in Fig. A1, H (1); of different shape (0).

58) as in Fig. A1, I (1); of different shape (0).

59) apical margin three- or slightly five-toothed with medial tooth strongest and lateral teeth bent inwards; of different shape (0).

60) Posterior margin of tergum 7 of male raised to a transverse keel crossing uninterruptedly below the medial tooth (1); keel interrupted, keel absent or medial tooth lacking (0).

61) Hairs of the metasomal scopa narrowly to broadly winged at two sides along their apical half and branched (2); narrowly to broadly winged at one side, not branched (1); neither winged nor branched (0).

62) Hairs of the metasomal scopa with small knobs at one side along their apical half ("sois à nodosités" according to Pasteels & Pasteels (1974)) and with a club-shaped apex (2); with small knobs and a pointed apex (1); without small knobs (0).

63) Apex of the hairs of the metasomal scopa very long and thin (1); without long and thin apex (0).

64) Apical half of the hairs of the metasomal scopa wavy to a higher or lesser degree (1); more or less straight (0).

65) Metasomal scopa white-colored with black triangle posteriorly (1); not two-colored (0).

66) Sternum 2 of male at least anteriorly with feltlike pubescence of fine and short hairs (1); normally haired (0).

67) Anterior portion of sternum 3 of male with feltlike pubescence of fine and short hairs (1); normally haired (0).

68) Sterna 2, 3, and 4 of male with dense fringe of long, white hairs (1); without dense fringe of long hairs (0).

69) Sternum 3 of male with rows of curled hairs posteriorly (1); without curled hairs (0).

70) Posterior margin of sternum 3 of male distinctly notched medially (1); straight or slightly incurved (0).

71) Posterior margin of sternum 4 of male with row of black thorns medially (1); without row of black thorns (0).

72) Sternum 4 of male with two lateral teeth formed by the posterior margin (1); teeth absent or if present arising from behind the posterior margin (0).

73) Sterna 4 and 5 of male with two lateral teeth arising from behind the posterior margin (1); teeth absent or if present not developed on both sterna or formed by the posterior margin (0).

74) Sternum 5 with two lateral teeth arising from behind the posterior margin, sternum 4 without teeth or provided with two lateral ridges only (1); teeth absent or if present distinctly developed also on sternum 4 or formed by the posterior margin (0).

75) Posterior margin of sternum 5 of male with row of black thorns medially (1); without row of black thorns (0).

76) Sternum 5 of male with two long lateral processes provided apically with a comb of bristles (2); with two lateral processes without comb (1); without lateral processes (0).

77) Posterior margin of sternum 5 of male with two short medial processes provided apically with a comb of bristles (2); processes absent, but combs present (1); processes and combs absent (0).

78) Sternum 5 of male deeply cut in and along the converging margins with a row of strong bristles (1); sternum 5 of different shape (0).

79) Sternum 5 of male narrow with thin, parallel-sided medial portion (1); sternum 5 broader and medial portion distinctly wider (0).

80) Sternum 6 of male with two teeth arising from behind the posterior margin (1); teeth absent or if present formed by the posterior margin (0).

81) Sternum 6 of male with two teeth formed by the posterior margin (1); teeth absent or if present arising from behind the posterior margin (0).

82) Sternum 6 of male with elevated longitudinal ridge (1); without ridge (0).

83) Sternum 6 of female with orange-colored thorns (1); without thorns (0).

84) Sternum 6 of female with subapical margin, area between subapical and apical margin densely haired (1); without subapical margin (0).

85) Subapical margin of sternum 6 of female with tooth medially (1); without tooth (0).

86) Subapical margin of sternum 6 of female with two lateral teeth (1); without teeth (0).

87) Medial width of sternum 7 of male: medial portion lacking (4); very narrow (3); rather narrow (2); rather broad (1); very broad (0).

88–92) Shape of sternum 8 of male:

88) as in Fig. A1, K (1); of different shape (0).

89) as in Fig. A1, L (1); of different shape (0).

90) as in Fig. A1, M (2); as in Fig. A1, N (1); of different shape (0).

91) as in Fig. A1, O (1); of different shape (0).

92) as in Fig. A1, P (1); of different shape (0).

93) Sternum 8 of male with long and slender, parallel-sided posterior process (1); process absent or if present not long and parallel-sided (0).

94) Gonocoxite provided with two teeth dorsally (1); without teeth (0).

95) Ventral process projecting at the apex of the gonocoxite deformed and strongly turned between gonostylus and penis valve (2); ventral process flat and strongly turned between gonostylus and penis valve (1); ventral process absent or if present not turned between gonostylus and penis valve or only very slightly so (0).

96) Ventral process projecting at the apex of the gonocoxite two-lobed (1); ventral process absent or if present not two-lobed (0).

97) Ventral process projecting at the apex of the gonocoxite as long as two-third of gonostylus length (1); ventral process absent or if present much shorter (0).

98) Ventral process projecting at the apex of the gonocoxite distinctly hooked apically (1); not hooked (0).

99) Penis valves widely separated basally, united by a long, narrow bridge (1); close together or fused basally, bridge therefore very short or absent (0).

100) Bridge basally connecting the penis valves with two sharp, triangular teeth laterally (2); with two rounded teeth laterally (1); without teeth (0).

101) Gonostylus absent (2); very slender (1); normally sized (0).

102) Gonostylus two-pronged in obtuse angle (1); of different shape (0).

103) Gonostylus two-pronged in acute angle (1); of different shape (0).

104) Ventral side of gonostylus with a dense, strongly localized tuft of hairs apically (1); without tuft of hairs (0).

105) Gonostylus with a row of long, stiff hairs directed inwards (1); without hairs or with short hairs only (0).

106) Dorsal side of penis valve on its whole length concave with elevated border (1); not concave on its whole length (0).

107) Penis valve provided with a long and slender, hammer-like process apically (1); without a hammer-like process (0).

108) Lower apex of penis valve with dense tuft of hairs dorsally (1); without tuft of hairs (0).

109) Apical portion of ventral process of penis valve turned down (1); ventral process absent or if present its apical portion not turned down (0).

110) Ventral side of penis valves with two black, roundish-to-oval small plates (1); without black small plates (0).

111) Black, roundish-to-oval small plate on ventral side of penis valve with deep groove (1); black plate absent or if present not grooved (0).

112) Principal nest building material: resin (1); other material (0).

113) Principal nest building material: plant wool (1); other material (0).

114) Resinous brood cells covered with a layer of leaf stripes (1); brood cells composed of pure resin partially mixed with small amounts of plant fibers or consisting of plant wool (0).

115) Brood cells built within empty snail shells (1); not within snail shells (0).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
A. arnoldi	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	1	0	1	1	0
H. aduncа	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0. rufa	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
0. submicans	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
M. willughbiella	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
M. pyrenaica	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T. pubescens	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	
T. laeviventre	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	
T. laticeps	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	
T. byssina	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	1	0	
T. dumerlei	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	1	0		
T. interrupta	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	1	0		
R. aculeatum	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	0	1	1	0		
R. caturigense	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	1	0		
R. exsectum	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	1	0		
R. superbum	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	0	1	1	0		
R. infuscatum	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	1	0	1	1	0		
R. buteum	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	1	0	1	1	0		
R. septemdentatum	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	1	0	1	1	0		
R. acuminatum	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	1	0	1	1	0		
R. siculum	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	1	0	1	1	0	1	1	0	
R. sticticum	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	1	0	1	1	0	1	1	0	
A. strigatum	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	1	1	1	1	
A. breviusculum	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	1	1	1	1	
A. troodicum	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	1	1	1	1	
E. judaeense	2	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	1	1	1	0	
E. clypeare	2	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	1	1	1	0	
E. nasicum	2	0	0	0	1	0	1	0	0	1	2	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	1	1	1	1	1	0	
E. insulare	2	0	0	0	1	0	1	0	0	1	2	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	1	1	1	0	
I. laterale	2	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	0	0	0	0	1	3	0	1	1	0	1	1	0
I. afrum	2	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	1	0	0	0	2	3	0	1	1	0	1	1	0
I. cimbiciforme	2	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	1	0	0	0	2	3	0	1	1	0	1	1	0
I. fedtschenkoi	2	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	1	0	0	0	0	2	0	1	1	0	1	1	0
I. grohmanni	2	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	1	0	0	0	0	1	0	1	1	0	1	1	0
I. ferrugineum	2	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	1	0	0	0	0	2	0	1	1	0	1	1	0
I. ovasi	2	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	1	0	0	0	0	1	0	1	1	0	1	1	0
I. limbiferum	2	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	1	0	0	0	0	1	0	1	1	0	1	1	0
A. alternans	2	0	0	1	1	0	0	0	1	0	0	1	0	0	0	0	0	1	1	0	1	0	1	0	0	0	0	0	1	1	0	1	1	0
A. pusillum	2	0	0	1	1	0	0	0	1	0	0	1	0	0	0	0	0	1	1	0	1	0	1	0	0	0	0	0	1	1	0	1	1	0
A. carduele	2	0	0	1	1	0	0	0	1	0	0	1	0	0	0	0	0	1	1	0	1	0	1	0	0	0	0	0	1	1	0	1	1	0
A. schulthessi	2	0	0	1	1	0	0	0	1	0	0	1	0	0	0	0	0	1	1	0	1	0	1	0	0	0	0	0	1	1	0	1	1	0
N. octodentatum	2	0	0	1	1	0	1	1	1	0	0	1	0	0	0	0	0	1	1	0	1	0	1	0	0	0	0	0	1	1	0	1	1	0
P. melanurum	2	0	0	1	1	0	0	1	1	0	0	1	0	0	0	0	0	1	1	0	1	0	1	0	0	0	0	0	1	1	0	1	1	0
P. rhombiferum	2	0	0	1	1	0	0	1	1	0	0	1	0	0	0	0	0	1	1	0	1	0	1	0	0	0	0	0	1	1	0	1	1	0
P. alpinum	2	0	0	1	1	0	0	1	1	0	0	1	0	0	0	0	0	1	1	0	1	0	1	0	0	0	0	0	1	1	0	1	1	0
P. lituratum	2	0	0	1	1	0	0	0	1	0	0	1	0	0	0	0	0	1	1	0	1	0	1	0	1	0	0	0	1	1	0	1	1	0
P. ochrognathum	2	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	1	1	0	1	0	1	0	1	0	0	0	1	1	0	1	1	0
P. reticulatum	2	0	0	1	1	0	0	1	1	0	0	1	0	0	0	0	0	1	1	0	1	0	1	0	0	0	0	0	1	1	0	1	1	0
P. eximium	2	0	0	1	1	0	0	0	1	0	0	1	0	0	0	0	0	1	1	0	1	0	1	0	0	1	0	1	1	1	0	1	1	0
P. wahrmannicum	2	0	0	1	1	0	0	0	1	0	0	1	0	0	0	0	0	1	1	0	1	0	1	0	0	2	0	1	1	1	0	1	1	0
A. pulchellum	2	0	0	2	1	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	1	0	0	0	0	0	1	1	0	1	1	0
A. echinatum	2	0	0	2	1	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	1	0	0	0	0	0	1	1	0	1	1	0
A. anguliventre	2	0	0	1	1	0	0	1	0	0	0	0	1	0	0	0	0	1	1	0	1	1	1	0	0	0	0	0	1	1	0	1	1	0
A. rotundum	2	0	0	1	1	0	0	1	0	0	0	0	1	0	0	0	0	0	1	1	0	1	0	1	0	0	0	0	0	1	1	0	1	1	0
A. undulatiforme	2	0	0	2	1	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	0	0	0	1	0	1	1	0	1	1	0
A. undulatum	2	0	0	2	1	0	0	1	1	0	0	0	0	0	0	0	0	1	1	1	1	0	1	0	0	0	1	0	1	1	0	1	1	0
A. oblongatum	2	0	0	2	1	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0	0	0	1	0	1	1	0	1	1	0
A. gussakovskiji	2	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	0
A. caspicum	2	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	0
A. diadema	2	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	0
A. spiniventre	2	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	0
A. luctuosum	2	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	0
A. trispinosum	2	0	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	0
A. auritum	2	0	0	1	1	0	0	1	0	0	0	0	0	0	0	1	0	1	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	0
A. punctatum	2	0	0	1	1	0	0	1	0	0	0	0	0	0	0	1	0	1	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	0
A. wüstneii	2	0	0	2	1	0	0	1	0	0	0	0	0	1	0	0	0	1	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	0
A. waltlii	2	0	0	2	1	0	0	1	0	0	0	0	0	1	0	0	0	1	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	0
A. tesselatum	2	0	0	1	1	0	0	1	0	0	0	0	0	1	0	0	0	1	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	0
A. montanum	2	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0	0	0	1	0	1	1	0	1	1	0
A. pullatum	2	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	1	0	1	1	0	1	1	0
A. cingulatum	2	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	1	0	1	1	0	1	1	0
A. taeniatum	2	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	1	0	1	1	0	1	1	0
A. loti	2	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	1	0	1	1	0	1	1	0
A. dalmaticum	2	0	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	1	0	1	1	0	1	1	0
A. manicatum	2	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	1	0	1	1	0	1	1	0
A. christianseni	2	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	1	0	1	1	0	1	1	0
A. septemspinosum	2	0	1	1	1	1	0	1	0	0	0	0	0	0	1	0	0	1	1	1	1	1	1	0	0	1	1	0	1	1	0	1	1	0
A. florentinum	2	0	1	1	1	1	0	1	0	0	0	0	0	0	1	0	0	1	1	1	1	1	1	0	0	1	1	0	1	1	0	1	1	0

APPENDIX 2

ta matrix for the cladistic analysis of the anthidiine bees. Unknown states are coded ?; in polymorphic species, both states are listed in the matr

31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77
0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0
0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0
0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1

in the matrix.

74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115
0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	1	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	1	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?
0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?
0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	
0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	?	?	?	?	?
0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0		
0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?
0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	?	?	?	?
0	1	0	0	0	0	0	1	0	0	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	?	?	?	?
1	1	0	0	0	0	0	1	0	0	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	1	
1	1	0	0	0	0	0	1	0	0	0	0	0	2	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	?	?	?	?	?
1	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	1	
1	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	1	?	?	?	?	?
1	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	0	0	1	
1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	0	0	1	
0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	
0	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	?	?	?	?	
0	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	?	?	?	?	?
0	0	0	0	0	0	0	0	0	0	1	1	1	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?
0	0	0	0	0	0	0	0	0	0	1	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?
0	0	0	0	0	0	1	0	0	0	1	1	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	?	?	?	?	?
1	0	0	0	0	0	0	0	0	0	1	1	1	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	?	?	?	?	?
0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	
0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?
0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?
0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?
0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	
0	0	0	0	0	0	1	0	0	0	0	0	0	3	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	?	?	?	?	?
0	0	0	0	0	0	0	1	0	0	0	0	0	3	0	0	0	0	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	?	?	?	?	?
0	0	0	0	0	0	1	0	0	0	0	0	0	3	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	?	?	?	?	?
0	0	0	0	0	1	0	1	0	0	0	0	0	3	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	?	?	?	?	?
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0	0	2	0	0	1	0	0	0	0	0	0	0	3	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?
0	0	2	2	0	1	0	0	0	0	0	0	0	3	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0		
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0	0	0	0	0	1	1	0	0	0	0	0	0	3	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	?	?	?	?	?
0	0	0	0	0	1	1	0	0	0	0	0	0	3	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	?	?	?	?	?
0	0	0	0	0	1	?	?	0	0	0	0	0	3	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	?	?	?	?	?
0	0	0	0	0	0	1	0	0	0	0	0	0	3	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?
0	0	0	0	0	0	1	0	0	0	0	0	0	3	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?
0	0	0	0	0	0	1	0	1	0	0	0	0	3	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?
0	0	0	0	0	0	1	0	0	0	0	0	0	3	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?
0	0	0	0	0	0	1	0	0	0	0	0	0	3	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?
0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	1	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?
0	0	0	0	0	0	1	0	0	0	0	0	0	3	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0			
0	0	0	0	0	0	1	0	0	0	0	0	0	3	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?
0	0	0	0	0	0	1	0	0	0	0	0	0	3	0	0	0	0	1	0	0	1	0	0	0	1	2	0	0	0	0	0	0	1	0	0	0	?	?	?	?	?
0	0	0	0	0	0	1	0	0	0	0	0	0	3	0	0	0	0	1	0	0	1	0	0	0	1	2	0	0	0	0	0	0	1	0	0	0	?	?	?	?	?
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0	0	0	0	0	0	0	1	0	0	0	0	0	3	0	0	0	0	1	0	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?
0	0	0	0	0	0	0	1	0	0	0	0	0	3	0	0	0	0	1	0	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?
0	0	0	0	0	0	0	1	0	0	0	0	0	3	0	0	0	0	1	0	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?
0	0	0	0	0	0	0	1	0	0	0	0	0	3	0	0	0	0	1	0	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?
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0	0	0	0	0	0	0	1	0	0	0	0	0	3	0	0	0	0	1	0	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0		
0	0	0	0	0	0	0	1	0	0	0	0	0	3	0	0	0	0	1	0	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?